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BIRD MIGRATION FROM THE POINT OF VIEW OF LIGHT AND LENGTH OF DAY CHANGES

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THE migration movements of birds very early excited the attention and curiosity of men. Various have been the myths and fanciful theories that have arisen to explain where the birds go, and what urges them to come and go. When considered from the modern, scientific point of view, there are several angles to the problem. One may ask where they go, how they go or guide themselves, and what urges them to go. These are all separate and legitimate aspects of those wonderful seasonal movements of the birds we have termed migration, but they are not equally simple in their solution.

Where the birds go in their autumnal movement to pass the winter has profoundly interested men from the earliest times. There was a time when it was believed they flew to the moon, and Cotton Mather (1714 and 1731), of New England, went so far as to put himself on record. Speaking of the disappearance of the wild pigeons, he believed they repaired "to some undiscovered satellite, accompanying the earth at a near distance." The moon appeared a little too distant, it would seem, so his satellite theory was invented to make the migrating journeys a little more probable. There was a time not so far back when men and even good scientists of their day were convinced that swallows buried themselves in the mud of ponds and lakes, or even hibernated

during the winter in a more or less benumbed or frozen condition in the hollow of trees. There are many references in the ancient literature of early writers on the subject of migration. Some men among them, notably Benjamin Smith Barton, were far ahead of their times in the matter of thinking correctly about the fall disappearance and migrations of certain birds. The noteworthy and original Barton (1799) deemed the idea of swallows hibernating in mud an erroneous one, and deplored the fact that this idea was actually gaining ground among the colonists. Strangely enough, Barton at times felt somewhat disturbed at the array of facts adduced purporting to show that swallows really hibernated in the mud, and he even agreed that it *might* be a very exceptional behavior. After all, how many of us to-day as scientists have similar feelings of doubt about our position, and do not hesitate now and then to hedge ourselves in a little to justify our views if need be.

The question as to where the birds migrate has been greatly cleared up since Barton's day, but we must give Barton credit for being a man of exceptional good sense and scientific ability for those troublesome pioneer times. With few exceptions, perhaps, it is now pretty well known where most birds go when they leave their summer homes, and it is but a question of time when the winter home of all will be known, for this is a simple problem of locality determination, capable of complete solution.

The question as to how the birds find their way is not as simple, not as easily subjected to convincing experimental proof, for some form of an obscure sensing of direction may come in, or a judgment or tropistic response to an unknown force or condition we have not yet thoroughly determined. It is enough to say that birds are guided by some directive stimulus, however, although this may not yet be entirely clear to the observer.

The great question which has led to many theories is: Why do birds migrate? What is the stimulus to the urge? There may be many reasons, among these the

matter of available food. This in winter time would send our starlings from their roosts in the cities to the surrounding country to forage each day, perhaps many miles away. The memory of their roosts with the oncoming of night would send them back again in the evening. This is simple enough, and is purely a local backward and forward movement, incumbent upon the daily necessities of existence. This may send birds into other regions if food is scarce, or conditions are unfavorable to their well-being. I have found flocks of bluebirds in the swamps in the Washington region in winter time feeding upon the dogwood berries. It might lead robins to congregate in the warmer portions of the south for the winter for the same reason. However, this is a minor phase of those great southward migratory movements which send thousands of other birds into the tropics or far beyond the tropics into the Southern Hemisphere with a preceding restlessness and a definite urge that nothing seems to satisfy except the southern trip. It is this great universal seasonal phase of migration that has baffled and still sorely baffles men for a reasonable answer.

The ice age theory finally came into its own, purporting to explain it all gracefully as an inherited habit, the result of a great polar icecap crowding the northern birds southward by its southern movements. To sustain such a theory involves a transmission of the memory impulse in an active state for thousands and tens of thousands of generations of birds. The icecap, granting its reality and extension slowly over the ancient northern abodes of the birds, found them stationary, with no seasonal migrations such as exist to-day. We are told the ice movements occupied not a lifetime of a bird nor the lifetime of a few descending generations, but thousands of years. How then could there be any remembrance of a former more northern home in the mind of any generation of birds? With southward movements of the ice and cold progressing so slowly, there would be no noticeable changes of abode southward for any generation, or even

for a hundred succeeding generations for that matter. Such are the difficulties of this ice-age theory to account for the beginnings of migration. It is but natural that these insurmountable difficulties should have been seen, and inherited memories dragged in to bolster up the weakness of the theory. The fatal weakness, however, is the memory stimulus, for memory is not likely to operate unless the experience of changed conditions has been within the lifetime of the individual. If it were granted the ice-age had happened as a sudden and cataclysmic advance southward, crowding the bird populations of the region precipitately toward the equatorial regions in the lifetime of living individuals, then the memory stimulus would have seemed more reasonable. This would have allowed an imparting of the original movement to the young of succeeding generations, not through the germ-cells by hereditary processes, but by direct associational movements between parents and offspring, as may actually occur to-day. Even here, however, the recession of the icecap, and the subsequent return of the birds to their former areas, would require a similar line of reasoning to make it sound. In spite of this the ice-age theory has been firmly entrenched even in the pages of some of our modern text-books of biology, and Frank M. Chapman (1897, p. 49) says: "There is good reason, therefore, for the belief that the necessity of securing a home in which their young could be reared was, as it is still, the cause of migration." It must be remembered, however, that birds have been migrating for ages, and that the present conditions are the result of numerous and important climatic changes. Chief among these is doubtless the Glacial Period. Indeed, Dr. Allen has stated, and the theory has been generally accepted, "that the migration of birds was the outcome of the Glacial Period." I myself was tutored in the theory as if it were an unquestionable fact, and I had to live many years before I could discover independently its weaknesses. If all our theories were taught sincerely and honestly as mere attempts

to explain what we do not know; if their strength and weaknesses were considered impartially at the time the theories were propounded, they would rarely stultify the mind into an unquestioning silence, and many would be deservedly short-lived. If one renounces the ice-age stimulus in the origin of the inborn habit of migration, what have we left? Who knows that we have an inborn habit of migration as some are wont to believe so implicitly? Why term it an inherited habit when it may be just as truly the result of an immediate stimulus of some fixed seasonal factor. An inherited habit demands a past, and the past must still have recourse to an unusual and initial stimulus. That is why the ice-age theory came into existence, because men implicitly regarded migration as an ingrained habit; it was a major premise in their reasoning. However, there is nothing whatever to prove that it is an inborn racial habit. There is quite as good reason, even more in keeping with the modern views of living behavior, to believe that migration is an annually induced movement.

Temperature has been put forth as a factor causing birds to migrate. Unfavorable temperatures unquestionably affect the comfort and welfare of birds, but why should the swallow show restlessness shortly after the first of July? Surely cold is not making them restless, yet that weird preparatory restlessness of the migration urge begins to assert itself even before the higher temperatures of the summer may have been reached. On the other hand, let us grant the cold tends to drive them southward into warmer regions for the winter. What then drives them northward with the same obsessing urge in springtime, forcing them into northern latitudes, oftentimes in advance of the northward swing of favorable isotherms, so that they suffer severely or may be frozen to death in the very region they left early the preceding autumn, supposedly to escape the oncoming of the autumn cold. Many birds leave at a higher mean temperature level in late summer and autumn than the mean

temperature prevailing on their arrival in spring. It is said the robin's migratory movements are determined by a temperature of 35° Fahrenheit, yet something makes him quietly forget this so-called determining point in the south throughout the winter until the spring urge affects him and away he goes, actually to be benumbed and nearly frozen to death in New England, leaving safer and more agreeable weather conditions behind. Why is he driven to subject himself to temperatures below the critical 35° with such haste and wantonness? These are the facts that make a temperature factor responsible for the migration impulse somewhat difficult to reconcile with the migrating moods of the birds.

Some have suggested light and length-of-day as an impelling factor. This suggestion is due some candid consideration from the viewpoint of recent studies with plant growth and reproduction as affected by different periods of daylight and darkness. It is known that birds are extremely sensitive to light. The whippoorwill does not want merely the blackness of night but a soft uncertain light. He is crepuscular and prefers a certain low intensity of light to stimulate maximum activity. Our diurnal birds are quite as sensitive to their own definite levels of morning and evening light, it would appear from the observations of Horace W. Wright. It would seem that this specific measure of light intensity from physiological standards of their own determines very largely the order of their early morning awakening and singing. So specific has this become that some of the flycatchers, preeminent among these the wood pewee, have a unique so-called twilight song, reserved for the very beginnings of the new day and the very last glimmerings of the closing day. A vast amount of good observation can be adduced to prove this point, it would seem, and it is an essential point in any consideration of the factor of light entering into the migration stimulus.

The factor of light as a stimulus to migration is not a strictly modern one. George Edwards (1751) presented

"Some Thoughts on the Passage of Birds." He says Mark Catesby presented a paper which was read before one of the meetings of the Royal Society. In this, Catesby imagined that birds migrated to the southern hemisphere to reach a latitude similar to that under which the bird lived in the northern hemisphere. Edwards did not see the paper but remembered its content and wrote that Catesby believed that a bird departing from 60° north latitude to 60° south latitude "will meet not only with the same altitude of the sun, in both latitudes, provided the passage is made in September or March, but with nearly the same degrees of heat." Edwards was shocked at such a ridiculous theory, and held it was "contrary to all reason, and to the nature of things."

In the Academy, Vol. VI, 1874, p. 262, a brief anonymous paragraph appeared saying the helpless Swedish poet Runeberg from his observations of the migrations of birds in Finland had come to the conclusion that the birds went southward because they felt a longing for light. Coming as it did from the great Swedish poet, who died in 1877 at the age of seventy-three years, there is something beautiful in the suggestion, beautiful because science with its cold, modern viewpoints and methods scorning the glamor of poetry, may yet prove the poet's simple inspiration true in greater or less degree. Newton (1874) took a vigorous stand against this idea of Runeberg's, saying the birds were actually going into regions of less light in autumn, leaving as many did long before the autumnal equinox.

Seebohm (1888) in Germany also suggested that some of the arctic-breeding birds in the beginning may have migrated because they were searching for more light. E. A. Schäfer (1907) committed himself in an interesting way to the theory that daylight is the determining factor of bird migration. Schäfer's paper is one of the most readable of these earlier papers. He, however, based the migrations of birds upon the need of more hours of day-

light than the northern regions afforded in winter, or the tropics in summer, as he indicates in the statement: "Given a food supply adequate in nature and amount to maintain the species in any region, and sufficient light all the year round to procure it, there would be no need for migration." He does not favor the view that migration results from changes in the sexual state, for he says: "That it is a result of developmental changes in the sexual organs is improbable, since sexually immature individuals are also subject to the migratory tendency." He is speaking of the ancestors of the Charadriidae. Garner and Allard (1920) set forth their results with plants as influenced by the relative length of the day and night. While the data in this paper dealt entirely with plant life as affected by the factor of day and night in stimulating or checking growth and reproduction in plants, suggestions were made concerning the possible operation of the factor upon some of the behaviors of animal life in the following terms: "As to animal life nothing definite can be said, but it may be found eventually that the animal organism is capable of responding to the stimulus of certain day lengths. It has occurred to the writers that possibly the migration of birds furnishes an interesting illustration of this response. Direct response to a stimulus of this character would seem to be more nearly in line with modern teachings of biology than are theories which make it necessary to assume the operation of instinct or volition in some form as explaining the phenomena in question." T. M. Savage English (1923), apparently stimulated by the suggestion, brought out an interesting discussion of some possibilities of the problem. English, however, makes it a matter of nutrition, because of longer feeding hours in high latitudes. In his discussion it is indicated that tropical day-birds may habitually lay fewer eggs than closely related forms or species in northern latitudes. He speaks of the homing instinct as being "the actual drawing force behind the northward migration." While it may be quite true that there is a gen-

erally higher level of fecundity for northern migrating birds than for tropical sedentary birds, this would hold were there no migration movements, and we are still confronted with the beginnings of the impetus for the migrating species. Eifrig (1924) is strongly inclined to believe the key to the migration stimulus lies in the factor of the length-of-day stimulus. A. Landsborough Thomson (1924) in correspondence to the editor of the *Auk* is inclined to feel that this is not as important a factor as Eifrig would believe.

Some work has been attempted in a scientific solution of the question from the standpoint of the effect of length of day by William Rowan (1925–1926) working in Canada with the familiar snowbird (*Junco hyemalis*). Rowan's paper in 1926 contained a more complete discussion of his experiments with juncos and presented an excellent discussion of the various aspects of migration in birds and fishes. Much more must be done to prove conclusively what part this factor actually plays in initiating the migration of the birds and orienting them southward or northward as the case may be. It is a significant fact that migration is not a local but a world-wide phenomenon, and in some weird manner swings backward and forward in both hemispheres between the poles and the tropical belt with the northward and southward trend of the sun. If this world-wide mass-shifting of great groups of the bird populations with the altitude movements of the sun and the consequent seasonal swing is all a matter of coincidence year in and year out with almost unerring synchronism, it is a marvelously persistent mechanism of chance and coincidence.

Not all birds are migrants, and no theory demands that all birds should be. There are non-migrant species in every part of the world and this should be expected whatever the factor may be that stimulates migratory behavior in the more active migrants.

There are striking parallelisms of behavior between plants and animals at many points. Even where it has

been shown that the relative length of day and night may exert profound effects upon vegetative and reproductive behavior of plants, the degree of expression of one phase or the other depends entirely upon the species or even the variety or strain. This is most strikingly shown in the behavior of soybean varieties grown in the Washington region, some of which flower readily enough in response to either long or short days. Other varieties require a relatively short day to promote flowering, and the so-called latest varieties require a still greater shortening of the day length to induce flowering. Birds in their sensitivity to the values of light intensity, according to the observations of Wright and others, show that they react more or less definitely to certain intensity levels, with the day-loving birds at one extreme and the crepuscular and night-loving birds at the other extreme.

If an initiating stimulus to migration were some factor of the light as length of day, two phases of the migratory behavior must be considered in its relation to this stimulus, it would seem. We must have an awakening, a sensing of the change, with a consequent restlessness, and a subsequent direction stimulus. Merely to change a factor operating upon a bird's life so that it becomes restless in midsummer, as do the swallows, is not enough. It is not enough that an aimless traveling should arise; that traveling must be somehow directed, else the birds would wander northward as well as southward. The majority of migrating birds do not do this, although in a few instances some birds, as the egret, tend to wander northward after the breeding season. Birds show not only a marked sensitivity to light intensity in their normal life, but during their migrations by night they seem particularly sensitive to beams and points of light in the darkness, which amounts almost to a pure tropistic response, such as plants show when growing in the dark. Admit a tiny beam of light and the plant will grow toward it with an almost irresistible tendency. In the dark migrating birds will dash themselves to death

against the glass of the lighthouse, seemingly driven to follow even along the beam of the light to its origin. There seems to be an actual physiological change in the bird's nature at the time of migration in some respects; the bird appears to be obsessed with restlessness, moodiness, with even new relations to light and darkness quite in contrast with its behavior when calmly settled with a nest and family responsibilities. At this time there is a normal activity and quiescence synchronizing with daylight and darkness, but with the terrible urge of migration in its blood, its wings may carry it dashing along through the darkness itself, which only a few days before brought it to a condition of rest. There is much yet to be learned concerning the light tropisms of birds, and something of an increased tropistic sensitivity to light seems to drive the birds into our lighthouses, etc., during the obsessing migration passion.

Even though the ends of migration are beneficial to the birds this may have no causal relation to the actual stimulus. It may be of decided advantage to a plant to flower before frost in response to a naturally shortening summer day, but the end was not foreseen in the cause with the plant. This may be quite as true of the birds. It is an advantage for the summer birds to be urged southward toward warmer regions, and the birds profit by it, but it may be as unreasoning behavior as that of the soybeans appearing to foresee the cold of autumn. The birds survive because something has directed them in the right direction and they escape a whole array of unfavorable conditions.

There has been much discussion of an internal organization responsible for the migratory impulse, and some have laid stress upon this and little else. It seems to me this is thinking far back of the real issue. It is like saying there must be a bird before a bird can migrate. Surely there must be an internal organization sensitive to some stimulus, and there must be feet or wings to carry the bird, too. No one will deny all that, for it is as self-

evident as a mathematical truth. However, the internal physiological state, the presence of the hormone, the activity of the gonad or what not, means nothing unless it is activated in given directions by favorable external stimuli at some time.

Strangely enough, when we fall back too literally upon physiological states and hormone activities to explain the migrations of birds, we find about as many inconsistencies as when we think of it all in terms of definite temperature levels, food requirements, or what not. If the state of the sexual condition regulates it all, we find the birds driving southward with declining sexual tension, and driving northward in spring with an increasing sexual tension. This, it seems to me, is like showing that the birds are driven south by cold in autumn, and north by heat in the springtime. There are elements of incompatibilities in such reasoning that demand fair consideration. Dr. Alvin R. Cahn (1925), of the University of Illinois, has well stated the exactness of the rhythm of migration as follows: "The big waves of bird migration occur almost at the exact date year after year, irrespective of the weather to a very large extent. If external factors alone were responsible for migration the birds would arrive almost any time. But an organism among the higher forms has a definite cycle through which it passes; a very definite series of physiological states which are passed through in sequence and which are not materially hurried or retarded by slight changes in external conditions. Therefore, it is not surprising to find the migration waves occurring year after year with surprising regularity, and to find that year after year the same species are found in the same migration waves." A. Landsborough Thomson (1921, pp. 468–469) also emphasizes this wonderful regularity: "One thing seems obvious, and that is that migration is a far too complex and also a far too regular phenomenon to be created anew each season merely under stress of circumstances; moreover, it is known that migration begins before the need is in the least pressing."

We may consider the reproductive behavior of many plants in the same light, and we find that many of them have sequence of cycles as definite, with flowering dates as regular as the migratory activities of the birds. We might be as inclined to think it all a matter of internal physiology and hereditary habit if we had not readily changed it in many plants, showing that a definite factor, the relative length of day and night, can change the seemingly constant time relations of all the seasonal cycles of expression.

It is a significant fact of the greatest moment to realize that bird-migrations are so regular and rhythmic. This means that if any immediate stimulus is held responsible for the origin of it all, it, too, must recur annually with a precision with respect to dates that never occurs with such variable factors as temperatures, barometric pressures, wind velocities and directions, food relations, etc. There is no conceivable external factor that meets these rigid requirements the world over, except the swing of the sun northward and southward with its rhythmic seasonal round. It would well act not only as the initial stimulus in the midsummer restlessness preceding migration, but it is quite conceivable that the southern and northern swing of the sun can serve as well to orient the birds by some obscure directive influence, sending them always in the direction of the swing.

Whatever the external factor, there are many strange coincidences with these astronomically precise sun-movements and the behavior of the birds. In the summertime, shortly after the solstice in June, some species show the premonitory restlessness of the migration urge. In the far south the same restlessness follows the turn of the sun in December and January. Some species seem to find it necessary to experience the longest days of the high latitudes; others are content at the equator with relatively short days. All degrees of adjustment between these two extremes are found for many other species. One is reminded of long-day plants and short-day plants,

or those which find their optimum of reproductive activities under daylight durations exceeding twelve hours in the one instance, and below twelve hours in the other. This would seem an especially striking parallel when we realize that many of the bird migrants, nesting in the high latitudes of North America in the northern hemisphere, find their winter home in the extreme southern regions of South America. This is the marvelous behavior of the group of waders, including such birds as the snipes, sandpipers, phalaropes and plovers. Alexander Wetmore (1927) shows the regular rhythmic movements of these birds in the following words: "Thus, the southward flight of these travelers begins with the northern fall and follows the southern spring to the south, while the return journey, begun in the austral fall season, continues north of the Equator with the advance of northern spring." Speaking of the exodus from Argentina he says: "The northward migration began at the close of January, with a slight movement among golden plovers." If our own swallows early in July show a premonition of the migration urge that seems exceptional, Wetmore finds that the Hudsonian godwit (*Limosa haemastica*) has arrived in Argentina in big flocks as early as July 2 (1880), being the earliest birds to arrive, and, therefore, the most responsive to some external factor, it would seem, urging them to leave their North American summer home. These facts are simply adduced to show that if an immediate stimulus is involved in initiating the migratory-urge, it must be perceived almost simultaneously with the solstice, whether going southward from the northern breeding grounds of North America, or going northward from the region of winter rest in southern South America.

There are other interesting facts to be noted. The different species have their own sequences in leaving in both regions in the southward or northward movements. The Baird sandpipers may remain in their South American winter home until the end of April. The golden plover,

on the other hand, has been observed to begin its northern migration as early as January 23, and probably gets it well under way in early April. The stilt sandpiper (*Micropalama himantopus*) appears to have left southern South America by March 1. Similar differences in the time of departing of these and other birds from their northern breeding homes is a matter of common observation. Whether or not it is all a matter of timely coincidence, these schedules associate these birds with daylight periods of a certain duration, to say the least about the matter. If birds show definite relations to light-intensity values in their awakening and singing, and their evening retiring, and if migrating birds show rather definite associations with certain lengths of day in their movements, this may all be a matter of mere coincidence, and it may well not be. The fixity of it all, however, seems to suggest nice adjustments concerned with the specific conditions of illumination in the one case and of light-duration in the other. One wonders what is responsible for the ebb and flow of the sexual functions attending the breeding activities, and, incidentally, the migration-movements. Is this varying physiological state of the sexual organs merely an internal cyclic matter independent of external conditions, or is it more external than we have believed, and influenced by some factor of the environment, call it what we will? If conditions of relative length of daylight and darkness enter into the question at all, does it merely affect a previously developed internal condition of the sexual life, or is it also responsible for the initiation of these sexual states in some direct or indirect manner, at present not clear to us, until internal physiological habits, so to speak, have been set up by generations of inheritance? We have the physiological habit, as clear cut and cyclic as one pleases, but shall we dogmatically trace it all back to an ancient prehistoric causal condition, as some are wont to do when they impute the original migratory urge to an ice-age condition? Those are nice questions of the problem which one must some time consider.

Birds have very definite feeding habits, and there isn't much doubt but that the general nutritional state can be influenced by regulating the hours of daylight. As a consequence the seasonal fecundity of the bird as expressed in egg-laying would be changed perhaps. This seems a fact in actual practice with the domestic fowl where electric illumination used to supplement the short winter days appears to incite more active egg-laying tendencies during the winter period, which is normally a period of low egg-production. English is inclined to believe that nature is doing just the same thing with her wild birds, making the birds of northern latitudes tend to be more prolific in some instances than the tropical species, because of the longer days which they experience for feeding, etc. He says: "Taking it then as a fact that the number of eggs in a clutch is inclined to increase with the distance from the equator at which the parent birds are nesting, may not this increase have a direct connection with latitude, that is to say, with the number of hours of daylight available for obtaining food at the time of the year when the nestlings have to be fed?" G. M. Allen (1925) is favorably impressed with the suggestion since the general proposition would seem to hold for both the day-birds and the night-birds of high latitudes and the tropics. That is, if the day-birds of northern latitudes lay more eggs because the days are longer, enabling them to get more nutrition, the night time of the night-birds must be correspondingly shorter, so that they should be less prolific than their tropical relatives with a longer night. This actually seems to hold. As Allen says: "It is interesting to see that in night-birds the rule may work the other way, too; for in the north the nighthawk and whippoorwill lay but two eggs and their 'working night' is shorter than those tropical relatives, as the frogmouths, oil-birds, and other nighthawks that lay three or four eggs and have a longer night to work in."

Allen regards the suggestion of the dependence of the migration of birds upon the relative length of day and

night as worthy of consideration and says: "The suggestion is a good one despite objections that may arise. One might even add that the waning year with days already shorter in August is a cause of *southward* migration to keep pace with a longer day, more hours of activity, and shorter daily periods without food."

The matter of the longer hour of daylight as merely making for a better basic nutrition of the organism may not be all, however. There may be a specific stimulus somewhere in the longer or shorter durations, as has been shown for certain plants. If one calls it light-nutrition all well and good, but it must be remembered that sunlight appears to have marked effects upon organisms from the ultra-violet content alone. These invisible or chemical rays of the sun's energy are now known to be extremely important in animal physiology. When it is recalled that they constitute less than 1 per cent. of the total energy of the sun, and are still vital to the well-being of man, it is rather remarkable. It is stated by eminent authorities (Hess, 1926) that the human infant thrives better when deprived of the visible rays than when denied the ultra-violet portion of its energy. If the latter are wanting, rickets becomes a constitutional malady. Hess states that rickets is unknown in the tropics, but is prevalent in all northern latitudes. We are told ultra-violet energy is strongest in summer and least in winter. When one speaks of the effects of light upon the organism, he must think of the total of solar radiation, not of the visible spectrum alone. He must remember that the ultra-violet portion constitutes another invisible spectrum, with highly specific effects in parts of its range, especially since Hess has shown that . . . "a difference of about 25 millionths of a millimeter determines whether the rays are of specific curative value, or whether they are inert in relation to rickets." With respect to the ultra-violet radiation, it would appear that quality not quantity is the important thing, and the difference between tropical sunlight and the sunlight of

higher latitudes depends upon this, for it has been shown there may be little essential difference in the amount of actual sunshine between the winter months in northern latitudes and in some parts of the tropics. When it is known that the ultra-violet radiations act through activation of the cholesterol which is especially abundant in the superficial layers of the skin, it becomes no simple problem to know just how light affects the reproductive activities in birds.

According to Professor A. B. Klugh, of Canada, who presented his facts in a paper at the recent Nashville Meeting of the American Association for the Advancement of Science, the normal ultra-violet radiations of the sun may actually be deadly to some minute crustacean forms of sea-life. These creatures were long known to remain during the day at depths below ninety feet, coming up at night to feed. This was long a puzzle to biologists. It would seem to be a necessity of their lives to avoid these lethal ultra-violet radiations, and they do it by keeping a deep absorbing water-screen between themselves and the sun. Here do we have a migration with the daily movements of the sun, with some factor of light the stimulus, and incidentally, perhaps, the destructive ultra-violet radiations are avoided and the creatures survive. It is a striking parallelism with those autumnal flowers which escape cold by flowering in autumn, occurring, as we now know, in many instances to the responses of length of day. With these facts in mind, we have to do with matters of no small complexity when we speak boldly of the nutritional effects of solar energy upon the birds. If human infants are sensitive to ultra-violet light, perhaps birds, especially the nestling birds, are, and thus we can befuddle ourselves with doubts and plausible suggestions at every turn.

Much remains to be done in the matter before even a feeling of confidence can be had. Nutritional effects due to longer hours of feeding alone would involve the visible spectrum only. It is known, however, that the ultra-

violet or invisible radiation of the sun may influence the general health and welfare apart from this. These may in addition be a purely specific stimulating effect of some portion of the solar radiation, affecting growth and reproduction, or some phases of its cycles of ebb and flow.

The practical side of the question has come into prominence in attempts to regulate the seasonal egg-laying activities of the domestic fowl. Yet one wonders how far the matter has been scientifically investigated. There seem to be wonderful possibilities with the domestic fowl even for the scientist. If supplementing the short daylight periods of the wintertime with artificial illumination tends to push the summer egg-laying activities into the winter months, we should have a second comparable group of fowls given artificial short daylight periods throughout the summer, and the longer daylight periods in the wintertime. In other words, one is given to wonder if a complete reversal of the usual daylight durations of summer and winter could bring about an adjusted complete reversal of the egg-laying distribution. This would require methods for shortening the days in a more or less normal manner when they are beginning to lengthen, let us say at the time of the spring equinox. On the other hand, it would require lengthening by artificial illumination after the autumnal equinox, when they are normally shortening by daily decrements. Not only is there a practical issue involved, but likewise a scientific side, which would throw light on the matter of the suppression or activation of gonad activity by appropriate changes in length of day, paralleling the work of Rowan with some of our wild winter birds. It may be said that the summer fecundity of our domestic fowls is coincident with the summer fecundity of our wild birds, a rather strong and regular coincidence, to say the least. The problem of the adaptations of the domestic fowl alone to other regions, to the tropics, and to the reversed summer and winter seasons of the southern hemisphere would be

of interest. A knowledge of their responses and correlations would throw additional light upon the behavior of birds in general to the different lengths of day, and their relations to the reproductive activities.

Whatever the factors that govern bird migration, it does not seem good biological reasoning to place it all on a basis of an ancient, inherited rhythm. Life is more plastic than that. The established regularity of it all points strongly to a nice recurring regularity in some fixed external factors. No known factor fulfills this condition, except the swing of the sun, with its attendant long-day and short-day relations. The migration impulse is world-wide at a given season, reversed in the northern and southern hemispheres because summer and winter are always coincident in opposite hemispheres. If it is merely a matter of a fortuitous coincidence in these larger features, as well as in many minor points, it is all one of the most spectacular instances of chance that can be found befuddling men in the universe. Regular coincidences of such a nature, however, happening with the same precision, year after year, century after century, are likely to have vital relations and interactions. Such manifestations of life are likely to be a resultant of the cosmic swing rather than independent of it. Plants are now known to behave as a part of this cosmic swing of the sun's position with its attendant changes in the daylight durations constituting our seasons.

It is not enough to show that the simple, basic nutritional relations are modified by changes in length of day due to more or less hours of feeding. If the entire matter were as simple as this, various degrees of starvation should produce comparable effects, or at least effects of a more or less similar nature. However, it has been shown with plants that the length-of-day effects are of another order not readily related to any phase of soil-nutrition response. Feed a poinsettia or a Klondyke cosmos plant all you please with soil nutrients or soil

moisture, and you will perhaps merely change its vegetative expression, its stature and rapidity of growth. On the other hand, ten hours of daylight allowed a branch each day in a comparative short time causes the branch to develop the reproductive phase. It is quite possible that the birds are affected in a similar way by light.

It is not enough to show that the different phases of the reproductive activities are dependent upon a favorable length of day. The problem still remains to determine how this would direct the birds into the great regular northward and southward movements. A stimulus alone explains nothing; this might account for the premonitory restlessness, but there must be an external guiding factor following upon this. If light is responsible for this phase it would seem to lie in some tropistic response of the birds to the direction of the rays of illumination. In this connection it is particularly significant that migrating birds have shown themselves positively phototropic, tending to follow the very path of a lighthouse beam oftentimes.

In closing it may be stated that the present discussion is merely an attempt to survey the more recent aspects of bird migration in the light of a new and plausible suggestion that some aspects of light may prove to be the inciting cause. It is not an unconditional defense of any theory. Length-of-day or light has more than been put forward to account for migration. Even here the manner of its operation has been variously explained.

It is doubtful if the birds actively desire more light, as the wise old poet Runeberg mused. This is the psychological viewpoint. It is quite possible there is no consciousness of the end or usefulness to the race in the migration impulse at all, any more than it is necessary to assume that soybeans flowering in autumn foresee the usefulness of the behavior in forestalling cold. From the very nature of the case advancing cold is one of the ultimate accompanying necessities of a shortening day

attendant upon a southward receding sun. Whatever happens, therefore, in response to these changed light relations must precede the cold, whether it be in the behavior of birds, animals or plants.

It is to be questioned if it is all a mere matter of simple nutrition affecting the germ cells directly or indirectly, as English and others would have it. There still remain the potent invisible portions of the spectrum of the nature of the ultra-violet radiation or what not. Specific, stimulatory effects of light must also be considered as possibly operating independently of any basic level of food metabolism.

While some factor of light-duration may be found to stimulate or retard the reproductive activities, as Rowan appears to have found in the case of the snow bird (*Junco hyemalis*), it is not clear how this in itself can always send birds unerringly north in spring and south in fall. It is possible that the daily increments and decrements of light are in some manner appreciated by the migratory birds. This could well be true since it is known that the birds in their morning awakening and evening retiring appear to be influenced by particular intensity levels depending upon the species. At least is it evident that their morning and evening movements throughout the year are nicely regulated with the seasonal increments and decrements of daylight. Whatever the factors responsible for the urge shortly after the solstices wherever the birds may be, some powerful directive force of the nature of a tropism similar to that of a plant growing toward light seems to be in operation to send the birds northward or southward, as the case may be. Interesting is it in this connection to note that insects may have their cosmic tropisms. The common May beetles not alone fly into our lights, but they may under certain conditions show the same tropistic light response toward the brilliant twilights of the summertime. In the writer's experience this was a striking behavior of the May beetles flying over the pastures on the New England

farm at Oxford, Massachusetts, where he spent his youth in studying the wild life there. To say the least an open mind is necessary in the matter, even though the newer aspects of this theory are opposed to our older notion of a fixed internal rhythm, but unfortunately the scientist is likely to be as dogmatic and as bigoted in his views oftentimes as the man on the street.

It may be said with finality that the question will always be an open one until all these doubtful factors have been carefully and impartially examined, and their true bearing determined with respect to the sexual state and the migration urge and behavior. While some particular length of day may stimulate a physiological or sexual state attended by migration restlessness and the breeding fervor, there yet remains the matter of the directive stimulus in the northward and southward movements, and the immediate backward turning at the solstices. There would seem to be a tropistic guidance here, an orientation somehow so sensitive as to doom certain birds ever to follow the sun in its swing between the two tropics.

LITERATURE CITED

Allen, G. M.
1925. "Birds and Their Attributes."

Anonymous.
1874. Academy, Vol. VI, p. 262. (The Swedish poet Runeberg is mentioned as claiming the birds migrated because they longed for light.)

Barton, Benjamin Smith.
1799. "Fragments of the Natural History of Pennsylvania."

Cahn, R. Alvin.
1925. "The Migrations of Animals." AM. NAT., Vol. LIX, pp. 539–556.

Chapman, Frank M.
1897. "Bird-life."

Edwards, George.
1751. "A Natural History of Birds."

Eifrig, G.
1924. "Is Photoperiodism a Factor in the Migration of Birds?" *Auk*, Vol. 41, July, pp. 439–444.

English, T. M. S.
1923. "On the Greater Length of the Day in High Latitudes as a Reason for Spring Migration." *Ilis*, 11th ser., Vol. 5, July, pp. 418–423.

Garner, W. W., and Allard, H. A.
1920. "Effect of the Relative Length of Day and Night and Other Factors of the Environment on Growth and Reproduction in plants." *Jour. Agr. Res.*, Vol. 18, No. 11, pp. 553–606.

Hess, Alfred F.
1926. "The Newer Knowledge of the Physiological Action of Ultra-violet Rays." Proc. Am. Phil. Soc., Vol. LXV, No. 3, pp. 202–206.

Mather, Cotton.
1714. Trans. Royal Soc., V. 29, No. 339, 3rd par. p. 64.
1731. Trans. Royal Soc., Abridged Ed., V. 5, p. 161.

Newton, Alfred.
1874. "The Migration of Birds." *Nature*, Vol. 10, Sept. 24, pp. 415–416.

Rowan, William.
1925. "Relation of Light to Bird-migration and Developmental Changes." *Nature*, Vol. 115, April 4, pp. 494–495.
1926. "On Photoperiodism, Reproductive Periodity, and the Annual Migration of Birds and Certain Fishes." Proc. Boston Soc. Nat. Hist., Vol. 38, No. 6, pp. 147–189.

Schäfer, E. A.
1907. "On the Incidence of Daylight as a Determining Factor in Bird-migration." *Nature*, Vol. 77, Dec. 19, pp. 159–163.

Seebohm, Henry.
1888. "The Geographical Distribution of the Family Charadriidae." London.

Thomson, A. L.
1921. "Results of a Study of Bird-migration by the Marking Method." *Ilis*, 11th ser., Vol. 3, July, pp. 466–527.
1924. "Photoperiodism in Bird Migration." *Auk*, Vol. 41, Oct., pp. 639–641.

Wetmore, Alexander.
1927. "Our Migrant Shore Birds in Southern South America." Tech. Bull. No. 26, Oct., U. S. Dept. of Agri.

VARIATION AND CORRELATION IN SERIALLY SITUATED ORGANS IN INSECTS, FISHES AND BIRDS[1]

W. W. ALPATOV[2] AND A. M. BOSCHKO-STEPANENKO[3]

I

THE purpose of the present paper is to summarize some data collected by the senior author during his work as a privat docent and curator of the Zoological Museum of the University of Moscow.

In spite of the large amount of biometric work that has been done, there have been but few attempts to determine specifically the general rules of correlation in animals. Pearl and Clawson's (5) study of the crayfish had this purpose. Papers on the correlation problem originating from Pearson's laboratory have been concerned chiefly with human material, and other authors have, for the most part, attacked this particular problem only occasionally and incidentally. We shall not attempt to bring together all the separate coefficients of correlation scattered through the immense literature on biological variation.

II

Pyrrhocoris apterus L. (Hemiptera) was collected twice in 1922 and 1923 in the same basswood park situated at a distance of about ten miles from Moscow. The first sample, taken in July, 1922, consisted of males and females collected *in copula* and studied by one of the authors of the present article from the point of view of sexual selection (2). The number of pairs was 171. The

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second collection contained only males taken separately in October of the year 1923.

The ravens—*Corvus cornix* L. (♀)—were collected by A. M. Boschko-Stepanenko during the winter 1925–26 in one of the central parks of the city of Moscow. There was probably a kind of epidemic among the birds, because every morning it was possible to pick up several corpses of the birds from the surface of the deep snow which covered the ground at that time of the year. Autopsies showed a great percentage of the birds infected with parasitic worms (Nematodes).

The fowls (*Gallus domesticus* L.) were taken directly from a wholesale store in the Moscow central market. All the birds were taken from the same basket sent from a Middle Russian district known for its highly developed poultry farm industry. The birds belonged to the common Middle Russian unimproved race. It is highly probable that all birds were less than one year old, being killed before the Christmas holidays of the year 1925.

The material on the goose (*Anser albifrons* Scop.) was collected during the expedition of the Floating Marine Scientific Institute to the coast of Nowaja Zemlia in the Beluschja Bay (Barents Sea) in September, 1923, by the senior author of the present article, who was a member of the above-mentioned expedition. The birds were killed in mass quantity by the inhabitants of this island, "Samojeds." The sex of the birds was determined by dissection. It is probable that the mass of the birds represented the young generation of the corresponding summer.

The material on fishes (*Boreogadus saida* (Lepechin)) was collected during the same expedition by Professor W. Soldatov, and after the determination of sex kindly handed over to us. According to Professor Soldatov's opinion the group is very homogeneous in respect to age and contains not more than two or three different year-groups.

In all the mentioned species of birds and in *Boreo-*

gadus only the female sex was studied. The measurements of fishes were taken with the aid of dividers and read on a millimeter ruler. In measuring the bird extremities a sliding caliper—"Columbus"—was used. The phalanges of the bird legs were measured by placing the ends of the dividers at the distal end of each phalanx and on the left *processus lateralis,* which gave the maximal length of the bones, including the cartilages. The measurements and calculations on bugs and fishes were done by the senior of the authors, while those on birds are the work of Mr. Boschko-Stepanenko, *stud. rer. nat.* of the University of Moscow. The measurements of *Pyrrhocoris apterus* were made by means of a Zeiss "Objectschraubenmikrometer." The limits of the measurements are shown on Fig. 1.

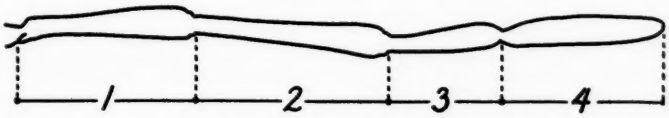

FIG. 1. Antenna of *Pyrrhocoris apterus* L. and the points of measurement.

III

The study of variation and correlation in *Pyrrhocoris,* an animal without growth during adult life, has a particular interest because, as was pointed out by one of the authors (1) in the case of the crayfish, we are dealing with a material not homogeneous in respect to the age.

Tables 1, 2 and 3 give us the biometrical constants for the length of joints of the antenna of *Pyrrhocoris apterus* L. The following constants have been calculated: averages, coefficients of variation, gross and partial coefficients of correlations. The indices of second, third and fourth joint expressed in percentages of the basal joint were calculated by means of the formula given by K. Pearson (6). It must be noted that sexual dimorphism exists in all characteristics, in absolute dimensions as well as in the proportions of the joints. No definite con-

TABLE 1

CONSTANTS OF VARIATION IN THE ANTENNAE OF *Pyrrhocoris apterus* L. ♂, 1922, N = 171. THE ARITHMETICAL MEANS ARE EXPRESSED IN MILLIMETERS

	Joint	1	2	3	4
Coefficient of correlation	1	1			
	2	0.770 ± .021	1		
	3	0.679 ± .028	0.783 ± .020	1	
	4	0.499 ± .039	0.577 ± .035	0.630 ± .031	1
Mean		1.3954 ± .0031	1.6627 ± .0042	1.0145 ± .0028	1.4344 ± .0030
Coefficient of variation		4.24 ± 0.16	4.86 ± .18	5.36 ± .20	4.09 ± .15
Index		100	119.24 ± .19	72.71 ± .15	103.14 ± .22
Partial C of correlation. Joint 1 made constant	2	—	1	—	—
	3	—	0.460 ± .041	1	—
	4	—	0.289 ± .047	0.459 ± .041	1

TABLE 2

CONSTANTS OF VARIATION IN THE ANTENNAE OF *Pyrrhocoris apterus* L. ♀, 1922, N = 171

	Joint	1	2	3	4
Coefficient of correlation	1	1			
	2	0.777 ± .021	1		
	3	0.590 ± .034	0.639 ± .031	1	
	4	0.427 ± .042	0.450 ± .041	0.548 ± .036	1
Mean		1.3329 ± .0028	1.6216 ± .0040	0.9933 ± .0033	1.4004 ± .0032
Coefficient of variation		4.12 ± .15	4.80 ± .18	6.36 ± .23	4.40 ± .16
Index		100	121.67 ± .19	74.63 ± .20	105.14 ± .25
Partial C of correlation. Joint 1 made constant	2	—	1	—	—
	3	—	0.354 ± .045	1	—
	4	—	0.215 ± .049	0.400 ± .043	—

TABLE 3

CONSTANTS OF VARIATION IN THE ANTENNAE OF *Pyrrhocoris apterus* L. ♂, 1923, N = 200

Joint	1	2	3	4
1	1			
2	0.850 ± .013	1		
3	0.715 ± .023	0.812 ± .016	1	
4	0.548 ± .033	0.547 ± .033	0.614 ± .030	1
Mean	1.2526 ± .0029	1.4801 ± .0036	0.9361 ± .0026	1.3836 ± .0033
Coefficient of variation	4.89 ± .16	5.09 ± .17	5.74 ± .19	4.95 ± .17
Index	100	118.19 ± .15	74.76 ± .15	110.58 ± .25

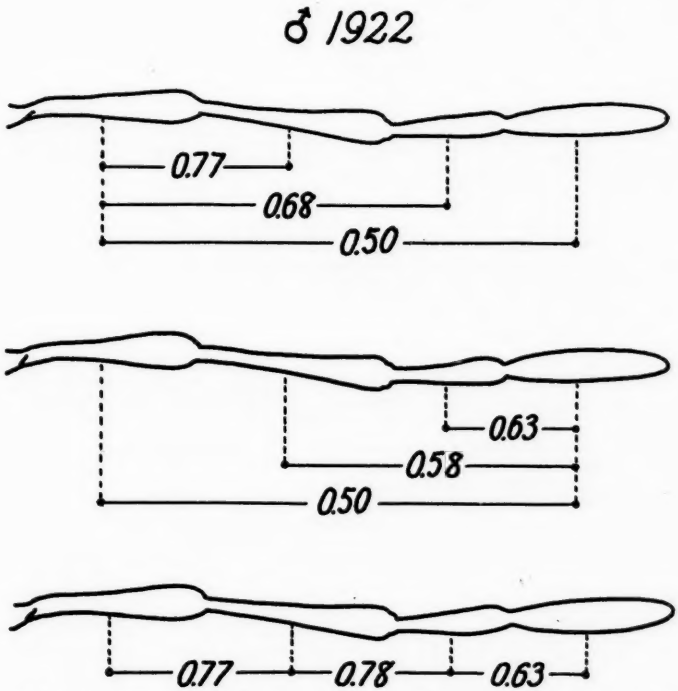

FIG. 2. Distribution of the correlation coefficients in the antenna of *Pyrrhocoris apterus* L., males, 1922.

clusions in respect to a higher variability of one or the other sex can be drawn. In all the three groups of insects the two middle joints are more variable than the basal and terminal ones. It must be noted that the males collected in 1923 differ from the males of the previous years in some respects. The joints are smaller, their

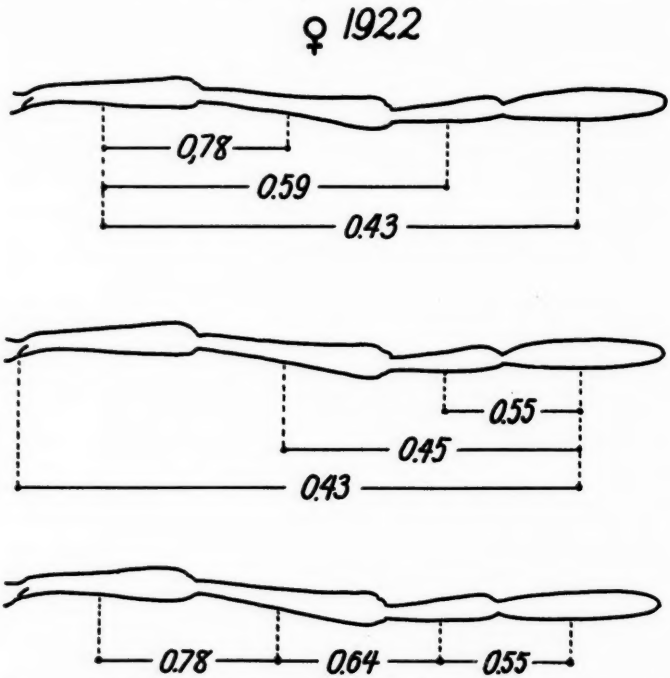

FIG. 3. Distribution of the correlation coefficients in the antenna of *Pyrrhocoris apterus* L., females, 1922.

variation higher, the proportions are different. No explanation is available at the present moment. Either seasonal variation may be responsible for this or the fact that the groups of the year 1923 contained not perfectly grown insects (animals with incompleted moultings), while the males of the year 1922 were collected *in copula* as fully developed animals. The coefficients of correla-

tion and certain regularities in the distributions of correlation over the antennae can be seen on diagrams 2, 3 and 4. The first correlation rule established by K. Pearson and his collaborators (4, 7) and confirmed by R. Pearl (5) in the crayfish is the rule of neighborhood. In our material this rule is also perfectly confirmed, the correlation of the first joint with the other diminishing

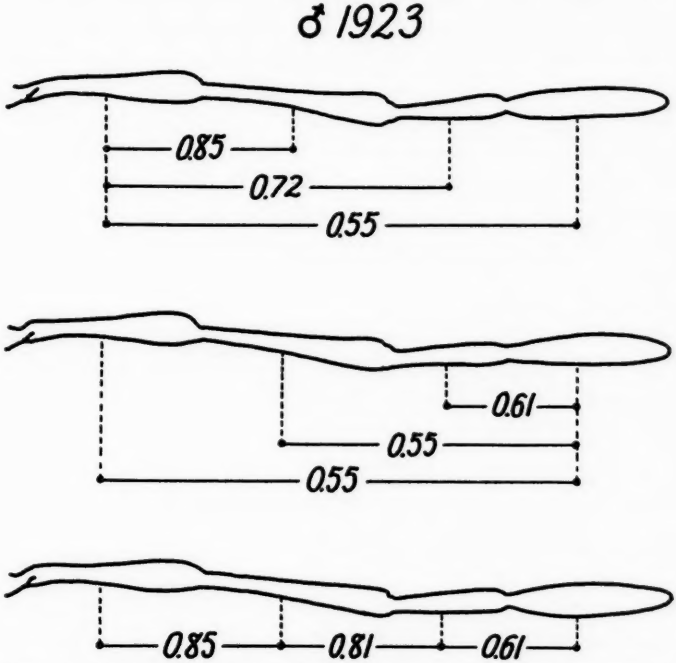

FIG. 4. Distribution of the correlation coefficients in the antenna of *Pyrrhocoris apterus*, males, 1923.

according to the distance between them. The same is true in the case of correlation of the terminal joint with other joints. The second and third diagrammatic representations in Figs. 2, 3 and 4 serve to establish another correlation rule. It can be seen that the correlations between the first joint and the second and third are

higher than those between the fourth, the third and the second. It appears, therefore, to be a rule that correlation is higher between proximal parts of the organ than in distal ones. In the group of males collected in 1923 the coefficients of correlation are higher than in the males and females of the previous years of collection. This is due probably to the higher degree of variation of the males of the year 1923. The partial coefficients of correlation, because of the reduction of the magnitude of the coefficients and the corresponding increase of probable errors, show only the existence of the rule of neighborhood.

IV

Tables 4, 5 and 6 give the averages and coefficients of correlation for the three species of birds. It is very

TABLE 4[4]

Corvus cornix L.

		Mean	Coefficient of variation	No. of cases
I	1	20.81 ± .08	4.14 ± .27	53
	2	14.45 ± .06	4.71 ± .31	54
II	1	11.99 ± .06	5.33 ± .34	56
	2	11.87 ± .05	4.83 ± .31	55
	3	10.19 ± .05	5.06 ± .33	54
III	1	11.98 ± .05	4.90 ± .32	55
	2	11.38 ± .05	4.42 ± .28	56
	3	12.70 ± .06	5.41 ± .34	56
	4	10.39 ± .05	4.96 ± .33	52
IV	1	7.29 ± .03	5.07 ± .33	55
	2	6.52 ± .03	4.51 ± .29	55
	3	6.48 ± .02	3.82 ± .24	56
	4	7.47 ± .05	6.76 ± .43	55
	5	7.83 ± .04	5.40 ± .35	53

interesting to note that the variation of the wild species —*Corvus cornix* and *Anser albifrons*—is lower than in the domestic fowl. Tables 7, 8 and 9 give all possible coefficients of correlation between the phalanges in each

[4] In this and the following tables on birds the Latin figures (I–IV) indicate the toes, the Arabic (1–5) the phalanges.

TABLE 5

Gallus domesticus L.

		Mean	Coefficient of variation	No. of cases
I	1	13.95 ± .10	9.04 ± .51	72
	2	8.65 ± .07	9.78 ± .56	69
II	1	18.44 ± .11	7.64 ± .42	75
	2	14.76 ± .08	7.17 ± .39	75
	3	11.15 ± .09	10.39 ± .58	73
III	1	19.23 ± .11	7.38 ± .41	73
	2	15.47 ± .09	7.47 ± .41	74
	3	14.16 ± .09	7.97 ± .45	72
	4	12.09 ± .10	9.90 ± .57	68
IV	1	13.48 ± .09	8.19 ± .45	75
	2	9.02 ± .05	7.19 ± .40	75
	3	7.84 ± .05	7.64 ± .42	75
	4	8.77 ± .07	9.68 ± .54	73
	5	9.37 ± .09	11.39 ± .67	65

TABLE 6

Anser albifrons Scop.[5]

		Mean	Coefficient of variation
I	1	11.73 ± .08	9.64 ± .50
	2	6.76 ± .03	8.06 ± .41
II	1	28.51 ± .09	4.15 ± .21
	2	19.92 ± .07	5.01 ± .26
	3	9.37 ± .05	6.42 ± .33
III	1	29.30 ± .08	3.86 ± .20
	2	19.89 ± .07	4.48 ± .23
	3	16.37 ± .08	5.63 ± .29
	4	10.32 ± .05	6.05 ± .31
IV	1	23.40 ± .07	4.42 ± .23
	2	15.21 ± .06	5.05 ± .26
	3	11.23 ± .04	5.21 ± .27
	4	12.23 ± .05	5.36 ± .27
	5	7.51 ± .04	7.95 ± .41

of the fingers. The rule of neighborhood is present in almost all the cases of the correlations of proximally situated phalanges. (The only exception is the low correlation coefficient between the first and second phalanges

[5] The number of cases in Anser is 87.

TABLE 7

Corvus cornix L.

IV	1	2	3	4	5
1	1				
2	0.529 ± .066	1			
3	0.636 ± .054	0.910 ± .016	1		
4	0.474 ± .071	0.462 ± .072	0.641 ± .054	1	
5	0.162 ± .091	0.279 ± .085	0.356 ± .080	0.225 ± .088	1

III	1	2	3	4
1	1			
2	0.857 ± .024	1		
3	0.579 ± .060	0.773 ± .036	1	
4	0.450 ± .075	0.480 ± .072	0.511 ± .069	1

II	1	2	3
1	1		
2	0.581 ± .060	1	
3	0.347 ± .081	0.571 ± .062	1

I	1	2
1	1	
2	0.599 ± .061	1

TABLE 8

Gallus domesticus L.

IV	1	2	3	4	5
1	1				
2	0.750 ± .034	1			
3	0.665 ± .043	0.711 ± .039	1		
4	0.494 ± .060	0.509 ± .058	0.625 ± .048	1	
5	0.385 ± .063	0.337 ± .065	0.502 ± .055	0.604 ± .047	1

III	1	2	3	4
1	1			
2	0.865 ± .020	1		
3	0.710 ± .040	0.905 ± .014	1	
4	0.527 ± .060	0.631 ± .050	0.664 ± .046	1

II	1	2	3
1	1		
2	0.858 ± .021	1	
3	0.558 ± .054	0.663 ± .044	1

I	1	2
1	1	
2	0.523 ± .055	1

of the IV toe in *Corvus.*) The correlation of distally situated joints is in accordance with our second rule—lower than in those situated proximally. The lower grade of these correlations increases naturally the prob-

TABLE 9

Anser albifrons Scop.

IV	1	2	3	4	5
1	1				
2	0.767 ± .030	1			
3	0.619 ± .045	0.836 ± .022	1		
4	0.618 ± .045	0.646 ± .042	0.672 ± .040	1	
5	0.288 ± .066	0.414 ± .060	0.331 ± .064	0.365 ± .063	1

III	1	2	3	4
1	1			
2	0.845 ± .021	1		
3	0.666 ± .040	0.807 ± .025	1	
4	0.132 ± .071	0.275 ± .067	0.286 ± .066	1

II	1	2	3
1	1		
2	0.725 ± .034	1	
3	0.102 ± .072	0.146 ± .071	1

I	1	2
1	1	
2	0.184 ± .070	1

able errors and produces, therefore, some irregularities in the rule of neighborhood, especially in the correlation of the IV toe. That is true for all species of birds dealt with.

V

Boreogadus saida (Lep.), belonging to the family Gadidae, was chosen because of the large number of the dorsal fins, furnishing a number of measurable characteristics. Table 10 shows the biometrical constants of the characters measured. Fig. 5 shows that there is a certain relation between the absolute size of the characters and its variability, expressed in terms of the coefficient of variation. The larger characters are less variable. Table 11 gives the coefficients of correlation which have

been calculated. In diagrammatic form they are represented on Figs. 6, 7, 8 and 9. The first striking fact is

TABLE 10

Boreogadus saida (LEPECH.). N = 100.
ARITHMETICAL MEANS IN MM.

No. of the character	Mean	Coefficient of variation
I*	53.74 ± .36	9.83 ± .47
II	22.41 ± .22	14.60 ± .71
III	8.15 ± .11	19.37 ± .96
IV	28.29 ± .25	12.94 ± .63
V	8.69 ± .12	19.74 ± .96
VI	30.62 ± .25	11.89 ± .57
VII	7.01 ± .08	17.62 ± .87
VIII	34.46 ± .31	13.32 ± .65
IX	6.26 ± .07	17.56 ± .86
X	30.07 ± .25	12.54 ± .61
XI	6.24 ± .09	22.44 ± 1.12
XII	31.85 ± .27	12.50 ± .61
XIII	85.99 ± .64	11.04 ± .53

* See Fig. 6.

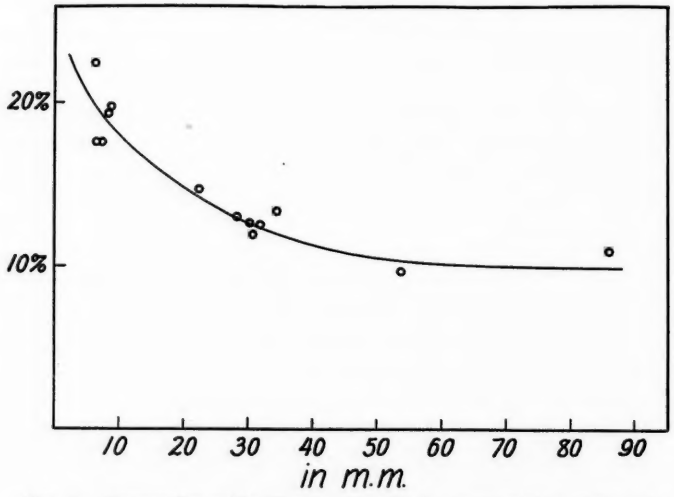

FIG. 5. *Boreogadus saida* (Lep.). Graphical representation of the relationship between the size of the characteristics (horizontal axis) and the coefficient of variation (vertical axis). The curve is fitted graphically.

TABLE 11

Boreogadus saida (LEPECHIN). COEFFICIENTS OF CORRELATION

	I	II	III	IV	V	VI	VII	VIII
I	1							
II	0.500 ± .051	1						
III	0.499 ± .051		1					
IV	0.744 ± .030			1				
V	0.454 ± .054				1			
VI	0.866 ± .017					1		
VII	0.493 ± .051						1	
VIII	0.921 ± 0.010	0.759 ± .029	0.446 ± .054	0.797 ± .025	0.403 ± .056	0.753 ± .029	0.477 ± .052	1

	XIII	VIII
VIII	0.925 ± .010	1
IX	0.348 ± .063	0.416 ± .056
X	0.817 ± .022	0.816 ± .022
XI	0.477 ± .052	0.442 ± .054
XII	0.820 ± .022	0.819 ± .022
XIII	1	0.925 ± .010

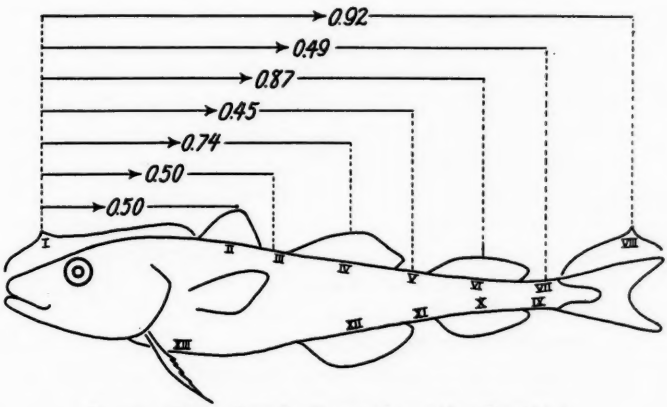

FIG. 6. Correlations in *Boreogadus saida* (Lepechin). Dorsal characteristics.

the low correlation between the "interfinal" lengths and other characters. This is true for the dorsal characters as well as for the ventral ones. The ante-dorsal distance is more highly correlated with the caudal fin and the second and third dorsal fins than with the first dorsal fin. The ante-anal distance is also higher correlated with the

caudal fin than with the closer situated first anal (0.925 ± .010 against 0.820 ± .022, diff. 0.105 ± .024, ratio = 4.37). We have here a disturbance of the rule of neighborhood, probably produced by some physiological and mechanical

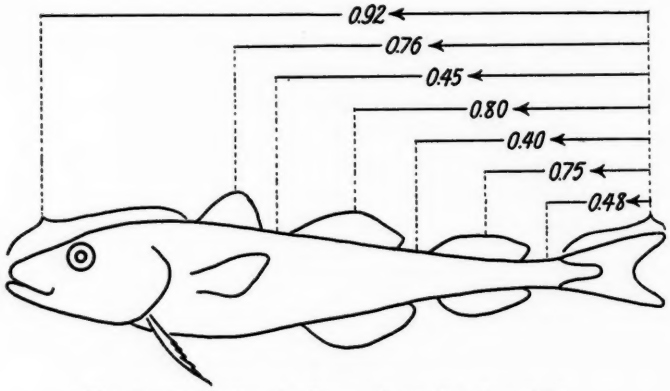

FIG. 7. Correlations in *Boreogadus saida* (Lepechin). Dorsal characteristics.

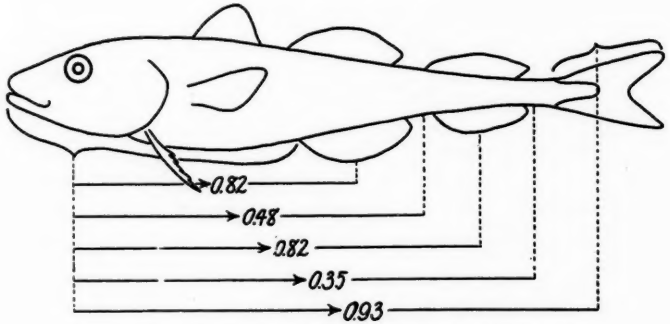

FIG. 8. Correlations in *Boreogadus saida* (Lepechin). Ventral characteristics.

causes influencing the correlated variation of the characters situated on the anterior part of the long axis of the body and on the caudal part of it.

The problem of organic correlation is frequently discussed in the biological literature, but we know very

little about the empirical laws which govern the phenomenon of correlation. The present paper is to be re-

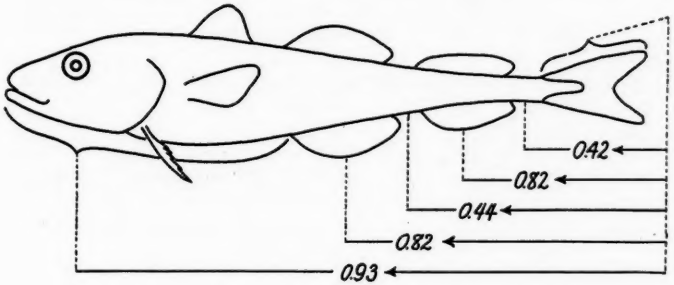

FIG. 9. Correlations in *Boreogadus saida* (Lepechin). Ventral characteristics.

garded as a small contribution in this field of biometrical research.

SUMMARY

The paper is devoted to a study of variation and correlation of the joints in the antennae of *Pyrrhocoris apterus* L. (Hemiptera), of the phalanges in three species of birds: *Gallus domesticus, Anser albifrons* and *Corvus cornix,* and of the fins of a fish, *Boreogadus saida* (Lep.).

The intercorrelations of the joint of the antennae of *Pyrrhocoris* give clear evidence of the existence of the rule of neighborhood (Pearson) and of a rule of greater correlation in proximal joints than in distal ones. This newly established rule is also observed in the correlations of the phalangeal bones of birds. The rule of neighborhood also holds in this case, with only one exception.

The correlations of ante-dorsal and ante-ventral lengths in the fish *Boreogadus saida,* with the length of the fins and the distances between them, show that the correlation between characters situated at opposite ends of the body (head and tail) is the largest. The rule of neighborhood does not appear in this case, being disturbed probably by mechanical or physiological causes.

LITERATURE CITED

(1) Alpatov, W. W.
1923. "Die Decapoden des Weissen, Barents und Karameeres" (in Russian with German summary). Berichte des Wissenschaftlichen Meeresinstituts, Lief. 7, pp. 1–36 in 4°.

(2) ————.
1925. Ueber die homogame und paragame Paarung in Tierreiche. Zool. Anzeiger, Bd. LVX, p. 329–331.

(3) ————.
1927. On the variability of the head appendages of insects (in Russian). Publ. of the 2d Russian Zool. Congress held in Moscow.

(4) Lewentz, M. A., and Whiteley, M. A.
1902. "A Second Study on the Variability and Correlation of the Hand." Biometrika, v. 1, pp. 345–360.

(5) Pearl, R., and Clawson, A. B.
1907. "Variation and Correlation in the Crayfish." Carnegie Institution of Washington. Publ. N. 64.

(6) Pearson, K.
1897. "On a Form of Spurious Correlations which Arise when Indices are Used in the Measurements of Organs." Proc. Roy. Soc., v. 60, pp. 489–498.

(7) Whiteley, M. A., and Pearson, K.
1900. "Data for the Problem of Evolution in Man. A First Study of the Variability and Correlation of the Hand." Proc. Roy. Soc., v. 65.

THE REPRODUCTIVE SYSTEM OF TRIPLOID INTERSEXES IN *DROSOPHILA MELANOGASTER*

TH. DOBZHANSKY AND C. B. BRIDGES

THE triploid intersexes in *Drosophila melanogaster* were found and were roughly described by Bridges (1921). At various times this description has been supplemented and references have been made to the great variability observed and to possible genetic modifiers (Morgan, Bridges and Sturtevant, 1925). We may now give the results of a more precise and detailed examination of this variability, with especial attention to the relative stability of the different parts of the reproductive system and to the relative time at which each develops in the pupal stage of the normal sexes.

The intersexes possess two X-chromosomes with three sets of autosomes, and the intersexual condition was interpreted as due to a genic balance or ratio of female determining genes to male determining genes (2X:3A) intermediate in value between the ratio in the normal female (2X:2A) and the modified ratio in the male (1X:2A). At first the variability was in part attributed to the presence of two or three of the small fourth chromosomes. Later, extended studies have lent no support to this hypothesis but have shown that the grade of development of the sexual characters is dependent upon genetic modifiers, whose location has not yet been exactly determined. The evidence is of two kinds: First, from an initial stock of triploids, 3N females were outcrossed separately to males from two diploid stocks. The 3N daughters from these crosses were again crossed to males like their fathers. This repeated outcrossing to two different stocks resulted in a shift in the grade of the intersexes in both cases, in the one case to a very high proportion of extreme male-type intersexes, and in the

other to nearly as high a proportion of extreme female-type intersexes. Second, an initial stock of triploids was subjected to selection and two lines were separated out, one of which had a high proportion of extreme male-type intersexes and the other a proportion of extreme female-type intersexes much higher than in the original stock but not so extreme a departure as that obtained in the selection toward maleness.

Measurements were made of certain secondary sexual characteristics, such as bristle length and various proportions of the bodies, and it was found that in most of these characteristics the intersexes are intermediate between true females on the one hand and true males on the other.

With respect to the reproductive system itself, the intersexes are, in a general way, intermediates, or better, mixtures in various proportions of male and female parts. Great variation is observed with respect to each

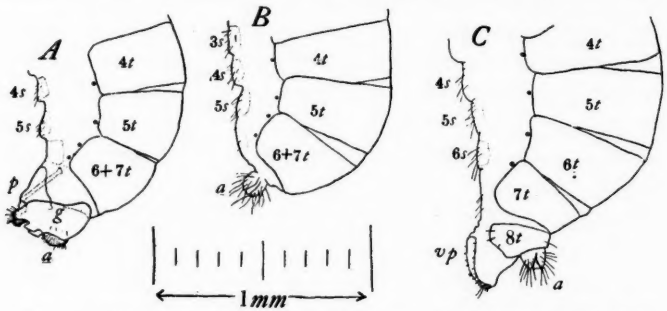

FIG. 1. Macerated and flattened abdomens. A, normal male; B, intersex; C, normal female. a, anal tubercle, with plates lateral in A and dorso-ventral in B and C; g, genital arch; p, penis apparatus; 3s–6s, third to sixth sternites; 4t–8t, fourth to eighth tergites; vp, vaginal plates, lateral.

separate feature of the sexual apparatus, which may be like that of the male, of the female, reduced or absent. The different parts tend to vary together and accordingly a given individual may be called more male-like or more female-like and be placed in one or another of a series of classes distinguishable between the most female-like on the one hand and the most male-like on the other. The

classes, of which seven can be clearly distinguished, are based upon the variations in the external features, but similar correlated variability occurs for the gonads, ducts, spermathecae and other internal features.

In the most male-like specimens of intersex the entire reproductive system differs from that of a true male only in that the testes are slightly less long and the spermatozoa produced are nonfunctional, apparently from immotility. In the classes that are progressively less male- and more female-like, the first part (beyond the two mentioned) to lose its distinctly male aspect is the anal tubercle (Figs. 1A and 3B), which, instead of having two simple lateral valves, now shows valves divided dorsoventrally also (into four half valves). Or, more usually, the two ventral half valves fuse to form a ventral valve of the female type, leaving the dorsal half valves separate. The dorsal half valves also fuse into a single dorsal valve, and this transformation into the typical female form (compare 3B with 3D) of anal tubercle is often complete before any other external feature shows the beginning of transformation.

The second external feature to change is the penis apparatus (Fig. 3A), which shows disappearance of accessory parts, a shortening and thickening with loss of definite form, an asymmetrical bending (Figs. 3C and 3E) and, finally, complete non-appearance. The penis apparatus disappears without being replaced by any homologous female representative.

The genital arch (united eighth and ninth tergites of the abdomen, nearly surrounding the penis and the anal tubercle, see Figs. 1A and 3B) loses its normal character, by becoming asymmetrically reduced (more reduced on the left, see Fig. 3D), by rotating (from the left, see Fig. 3F) to a position ventral to the anus instead of dorsal, and finally by disappearing entirely, without replacement by a corresponding female part (Fig. 1B).

Before the arch has completely disappeared, the internal genitalia have become affected. The testes shorten

from double spirals (Fig. 2A) to relatively small ellipsoids, then lose their attachment to the vasa deferentia and lie free in the body cavity (Fig. 2B). Even at their smallest they show the yellow color characteristic of

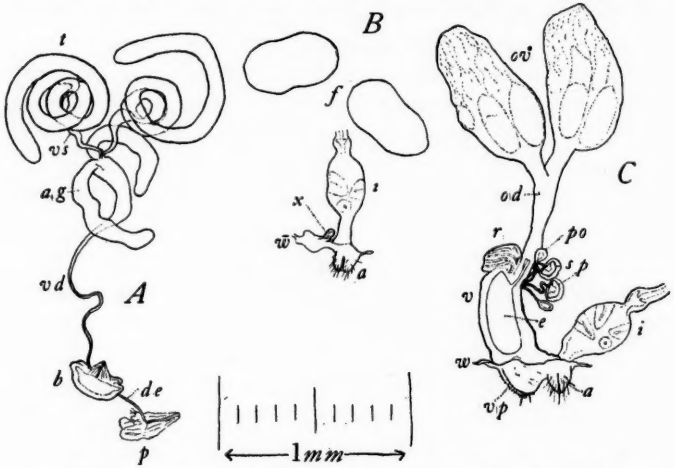

FIG. 2. Dissections of internal genitalia. A, normal male; B, intersex, at greatest reduction; C, normal female. a, anal tubercle; ag, accessory glands; b, bulbus ejaculatorius; de, ductus ejaculatorius; e, egg in vagina; f, free testes of ellipsoidal type; i, intestine with anal glands and valvae; od, oviduct, branched; ov, ovaries; p, penis apparatus; po, parovaria; r, receptacle, ventral; sp, spermathecae, paired; t, testes, paired; v, vagina; vd, vas deferens; vp, vaginal plates, lateral; vs, vesiculae seminales; w, body wall; x, vestige of genital apparatus.

testes. The genital ducts (vesiculae seminales, vas deferens, ductus ejaculatorius, bulbus ejaculatorius or "sperm pump" and the accessory glands) become reduced in size, at first asymmetrically, and finally are represented only by a very small bladder lying ventral to the anus (Fig. 2B). This bladder corresponds in position to the imaginal disk in the late larval stage but is even smaller, and is not of distinctive male or female type.

The reduction of the whole system of male reproductive organs is startling in its extent; only careful examination shows the rudiment of the disk beside the fully developed intestine and anal glands (Fig. 2B).

The first distinctively female organ to appear, aside from the nature of the anal tubercle, is the pair of spermathecae. In the most rudimentary form observed, the spermathecae were tiny bladders attached by a short divided duct to the rudimentary disk.

Next appear externally the pair of vaginal plates bordered with short stiff pines (Figs. 1C and 2C). The genitalia of the male and of the extreme male-type intersex, as seen posteriorly, are rotated counterclockwise

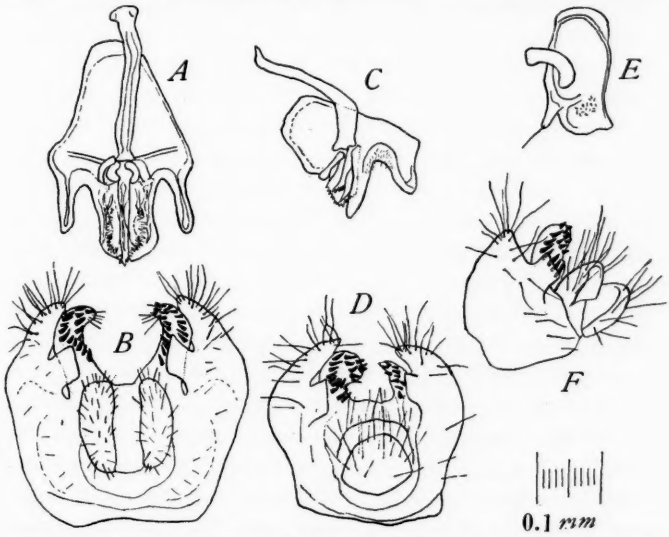

FIG. 3. Macerated parts of copulatory apparatus. A, penis apparatus of normal male; B, genital arch and anal tubercle with lateral plates of normal male; C, reduced and twisted penis apparatus of intersex; D, slightly reduced genital arch of the same intersex, anal plates dorso-ventral; E, reduced penis apparatus of another intersex, and reduced genital arch of same.

through 360°, so that the duct loops once about the intestine. This rotation is progressively undone in the passage to the female-type intersex. The first evidence of the loosening of rotation was the asymmetrical reduction of the arch and the bending of the penis (Figs. 3C and 3D). When the vaginal plates appear, they also are

asymmetrical, and in more female-like development complete the reversal into normal position.

The spermathecae appear before the vagina, to which they are normally attached, has appeared. The vagina then appears as an extension between the vaginal plates and the attachment of the ducts of the spermathecae. At practically the same time with the vagina appears the spirally coiled ventral receptacle, which soon becomes long. The parovaria likewise appear as small ducts with bulbous endings. Next appears the oviduct as a simple outpushing from the end of the vagina, and, in slightly more extreme female types, it lengthens and bifurcates (see Fig. 2C for normal relations of parts in female).

The gonads, which are still testicular in structure (that is, one-chambered, ellipsoidal yellow bodies), are now again attached weakly to the oviducts, often only one, the other being still free. The ellipsoidal testes never show development of spermatids and rarely show a maturation division. The testes attached to the oviducts show spermatogonial divisions and some growth of the spermatocytes. Next follow several stages of the transformation into ovaries. The first evidence of this is the presence of a few small chambers in addition to the main testicular chamber. The sections appear like those of a multiple testis. The accessory chambers increase in numbers, lengthen, become parallel and lose the yellow color characteristic of the testicular wall. Some intermediates present the appearance of an ovary with an outbudding ellipsoidal yellow testis. Often one gonad is a free yellow testis, while the other is an attached colorless ovary. The ovarial chambers show segments, simulating egg-strings, but the cells in the terminal chambers, corresponding to oögonia, are still like those in the free testis. But they are not arranged in successive layers, as they are about the primary spermatogonia in the more male-like gonads. In the more basal chambers the cells are like half-grown spermatocytes, or, eventually, growing nurse cells. Only in the most extreme female-type inter-

sexes is there differentiation of an egg-cell in the follicle and deposition of yolk. (For normal appearance of ovaries, see Fig. 2C.) All intersexes are sterile, both of the extreme male-type and of the extreme female-type.

The external features show accompanying changes. The black color, characteristic of the tip of the abdomen of the male, becomes flecked with light etching, and gradually breaks up into the banding characteristic of the female. The sixth and seventh tergites, fused in the male-type (Figs. 1A and 1B), split at one edge or separate entirely, as in the normal female. The rounded tip of the abdomen gives way to the pointed tip, as in the female. The cross-section of the abdomen changes from circular to flat beneath.

The last male characteristic to disappear is the male sex-comb, situated on the tarsi of the front legs. The number of spines may be reduced, or the whole row may disappear. The total disappearance of both sex-combs has been noted in only 2 or 3 per cent. of cases in the most highly selected female strain.

It will have been noticed that many of the distinctively male characters, especially the genital arch, penis, all genital ducts and accessories, are eliminated without transformation into organs characteristic of the female. Only later do the corresponding female organs develop from fresh outpushings from the imaginal disk. This behavior is different from what was formerly supposed to be the case, and seems also to be different from the situation in *Lymantria* (Goldschmidt, 1920).

The above description of the characters of the intersexes has been made in roughly the inverse order of the stability of the different male characteristics. Thus, the most stable male characteristic is the presence of the sex-combs. The order of stability of the female parts is the reverse of this; for the extreme male-type intersex is one in which the proportion of the male characteristics approaches 100 per cent., while the proportion of female characteristics approaches zero. Although the sex-combs

are the most stable male characteristic, they are the poorest index of maleness in the individual, existing in individuals in which the proportion of male characters is nearly zero, while the proportion of female characters is very high. Conversely, the best index of maleness is the least stable male characteristic, namely, the lateral disposition of the anal plates.

A more precise determination of the relative order of stability, and hence of their value as indices, was made for eleven male characteristics and eight female characteristics. About four hundred intersexes were dissected and were recorded with respect to the condition of each of the internal features. About four hundred other intersexes were classified with respect to certain external features. The condition of anal tubercle, genital arch, vaginal plates and spermathecae was recorded for all eight hundred. Finally, correlation coefficients were calculated, between all characters taken two at a time. The correlation coefficients were arranged in series from the most positive to the most negative. On the assumption that the correlation is greatest where stability and significance are most alike, this series gives the exact order of stability of the characteristics studied. In Table I the male and female characteristics are arranged in two series, in which, as noted above, the stability is in inverse order.

The order of stability of the characters might be expected to be definitely related to the relative times at which the sexual characters originated, developed and became fixed in pupal history. Goldschmidt found this to be true for the intersexes of *Lymantria* (Goldschmidt, 1920; contains references to earlier works back to 1911).

A study was made of the development of the reproductive system in the pupae of normal females and of normal males. Immediately following pupation, individuals were isolated. Dissections were made of such pupae, and of others at two-hour intervals in the development, until seventy hours had passed. The normal pupal develop-

TABLE I

Male characters	Age of pupa	Unstable
1. Anal plates lateral	50–52	∨
2. Penis normal in shape	44–46	↓
3. Testes spiral in form	30–32	↓
4. Testes connected with vas def.	26–28	↓
5. Genital arch normal in shape	26–28	↓
6. Penis present	24–26	↓
7. Male ducts present	22–24	↓
8. Genital arch present	18–20	↓
9. Gonads yellow	68–74	↓
10. VIth and VIIth tergites fused	— —[1]	↓
11. Sex-combs present	Before 20[1]	Stable

Female characters	Age of pupa	Stable
1. Anal plates dorso-ventral	44–46	∨
2. Chitinous spermathecae present	42–44	↓
3. Vaginal plates present	32–34	↓
4. Vagina present	24–26	↓
5. Ventral receptacle present	24–26	↓
6. Gonads ovarian in structure	2–4	↓
7. VIth and VIIth tergites free	— —[1]	↓
8. Sex-combs absent	Before 20[1]	Unstable

[1] Not yet exactly determined.

ment occupied eighty-six to ninety-eight hours at the temperature (27° C.) used.

The results show that a definite relation does exist between the order of stability of the characters and the lateness of development in pupal history. For the males, the late-developing characters are the least stable in the intersexes, and the most stable male characters of the intersexes are those that develop early in normal pupal history. For the females, the seriation is reversed: the characters that normally develop early are least stable in the intersexes and the characters that develop late are relatively stable. Two obvious exceptions were found: the too early development of the ovarian tubules and the too late development of the yellow color of the testes.

An explanation of this relation may be suggested, following in a general way the explanation advanced by Goldschmidt for *Lymantria* intersexes. Each intersex

may be supposed to develop up to a certain point as a male individual and thereafter as a female. The intersex becomes more female-like if the moment of reversal comes early in development and more male-like if the reversal occurs late. The range of variability in time and hence in degree of assumption of female characters is very great in *Drosophila* intersexes, probably because the balance of the opposing male and female determiners is very exactly intermediate between the critical values for complete femaleness and complete maleness.

It may be suggested that in the case of the two exceptions the development of the tissue is not limited to growth in the male direction and cessation of growth at the moment of reversal, but can proceed in the new direction. With the other male characters, for example, the ducts, development simply ceases at the moment of reversal, and thereafter new structures corresponding to the other sex are developed.

LITERATURE CITED

Bridges, C. B.
1921. "Triploid Intersexes in *Drosophila melanogaster*," *Science*, n. s., **54**: 252–254.

Goldschmidt, R.
1920. "Untersuchungen über Intersexualität." *Zeit. f. Ind. Abst. Vererb.*, **23**: 1–199.

Morgan, T. H., C. B. Bridges and A. H. Sturtevant.
1925. "The Genetics of *Drosophila*," *Bibliographia Genetica*, **2**: 1–262.

GENETICAL AND CYTOLOGICAL OBSERVATIONS ON *ORYZAEPHILUS SURINAMENSIS* (THE SAW-TOOTHED GRAIN BEETLE)

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BECAUSE of the importance to genetics of finding insects which lend themselves to genetical study as Drosophila has done, an attempt was made to find suitable material for this purpose. There are four main characters which such an insect should exhibit: (1) It must have visible heritable variations; (2) be easily raised in the laboratory; (3) the sex should be determinable by some well-defined external marking; and (4) in order to get the greatest number of generations the life cycle should be short and not a seasonal one.

Oryzaephilus surinamensis (saw-toothed grain beetle) has proved to be suitable for this work. This beetle gets its common name from the fact that it has a peculiar saw-toothed thorax. Normally there are six of these teeth on each lateral margin, all practically the same size and equally distributed. The position and number of these teeth or spines varied considerably, but only two of the many variations proved to be heritable. The male is distinguished from the female by an easily detected spine on the preaxial side of the hind leg. The insect is easily cultured and well adapted for laboratory conditions. The life cycle is short, taking from thirty to fifty days, depending on the conditions. The adult is dorso-ventrally flat, measuring from 2.5 to 3 millimeters in length and about .9 millimeters in width. At maturity it is a golden brown color, becoming darker as it grows older until it is nearly black.

Experimentally this insect has received slight attention. The only previous work of any significance was

done by Back and Cotton (26). They made a detailed study of its life history under various conditions, being interested in methods of its economic control.

Life History and Culture Methods

The larvae and adults both feed upon any vegetable food, especially on ground cereals. In these experiments the cultures were made up with ground corn. The consistency of the corn made it less liable to cake and mould than some of the other materials tried. General cultures were made up in half pint milk bottles and the test matings were made in shell vials. The cultures were kept in a "constant" temperature cabinet, which varied from 26° to 32° C., the optimum being 28°. The adults and larvae are unable to feed on food that is too dry. The food itself can not be moistened because it cakes and moulds immediately. Moistening the cotton plugs of the tubes also proved to be unsatisfactory for the same reason. The desired humidity was finally obtained by placing several milk bottles with water, with cotton wicks, in the compartment. With this arrangement mould never appeared and enough moisture was provided for the well-being of the cultures.

Under the above conditions a generation appears every 30 to 34 days. The duration of the different periods in the insect's life history is shown in the following table:

Egg hatches	3– 4 days
Larval stage	12–17 days
Prepupal stage	1 day
Sexual maturity	24–48 hours after emergence

The female begins to lay eggs five to seven days after emergence. The egg-laying period is from two to five months.

Before proceeding with the account of the experimental work I wish to express to Dr. F. B. Hanson my appreciation for his many helpful suggestions concerning breeding experiments. I am also indebted to Dr. Caswell Grave for suggestions which aided in my cytological work.

Experimental Data

The breeding experiments were started in February, 1927, with a stock obtained from the Bureau of Entomology. In a short time several variations in the number and position of the spines appeared. For convenience the spines were numbered 1 to 6, beginning at the anterior end of the thorax. If a spine is missing the remaining spines on that particular side are found in their natural positions, leaving a space where it should be. Almost any number or any combination of spines may be found missing. Such variations, however, proved to be purely somatic. Eight to nine per cent. of the individuals in the cultures showed these variations.

From a general stock of 5,719 individuals there were 2,613 males and 3,106 females. The sex ratio calculated from these data is 45.70 per cent. males, with a probable error of $\pm$ .50.

In a large count made the tenth of August two individuals were found having the same striking variation but differing from those noted before. These individuals had the normal number of spines, but the first three and the last three tended to be grouped together, leaving a wide space between spines 3 and 4. Spine 5 had partially fused with the sixth, giving the last spine on each side a broad base and two terminal points. Figs. 1 and 2 show the normal arrangement of the spines and the wide-spaced (W.S.) mutation. The two happened to be male and female and were mated, although the female was not virgin. The tube was not observed until six weeks later. Of the 122 individuals then obtained 55 showed the same peculiar spine arrangement the parents had exhibited. The only difference noted was that all the offspring did not show a fusion of the spines 5 and 6. It was found later that a fusion of the fifth and sixth spines did not necessarily accompany the W.S. character, but it could not be separated from it as a distinct character. Fig. 3 illustrates the thorax of a beetle with the W.S. character without a fusion of the fifth and sixth spines.

TABLE I

SHOWING THE SEPARATE COUNTS FROM CULTURE C, MATED 9/20/27. THE P_1 WAS 4 W.S. ♂♂ × 4 W.S. ♀♀ FROM THE FIRST W.S. MATING

Date	Normals			Variations		
	Males	Females	Totals	Males	Females	Totals
10/21/27	9	4	13	3	2	5
10/22/27	2	2	4	5	2	7
10/24/27	1	0	1	2	3	5
10/26/27	0	0	0	0	2	2
10/28/27	0	0	0	1	0	1
11/6/27	1	3	4	4	7	11
11/8/27	0	3	3	7	7	14
11/12/27	0	0	0	4	3	7
11/14/27	0	0	0	3	2	5
11/16/27	1	0	1	10	19	29
11/18/27	1	1	2	6	1	7
11/20/27	0	0	0	3	2	5
11/23/27	0	0	0	1	1	2
11/25/27	0	0	0	2	1	3
11/27/27	0	0	0	2	1	3
11/29/27	0	0	0	0	2	2
12/1/27	0	0	0	1	3	4
12/3/27	0	0	0	2	4	6
12/5/27	0	0	0	2	4	6
12/17/27	0	0	0	22	25	47
12/20/27	0	0	0	4	3	7
12/24/27	0	0	0	3	1	4
12/27/27	0	0	0	0	6	6
12/29/27	0	0	0	1	1	2
12/31/27	0	0	0	1	1	2
1/2/28	0	0	0	0	1	1
1/5/28	0	0	0	1	0	1

TABLE II

A TABLE SHOWING THE TOTALS FROM THE FOUR CULTURES

Culture	Normals			Variations		
	Males	Females	Totals	Males	Females	Totals
A	4	23	27	78	82	160
B	21	21	42	76	73	149
C	15	14	29	90	103	193
D	8	30	38	38	67	105
Totals	48	88	136	282	325	607

From these fifty-five mutants four cultures (A, B, C and D) of four pairs each were made. Since the females were not virgins normals were expected to appear in the

cultures. In Table I, using culture C as an example because of the greater numbers, during the first part of the counts normals occurred but by the end of the twenty-eighth day they ceased to appear. All the beetles in the cultures after about the twenty-eighth day had the W.S. character. Table II gives the totals of the four cultures. Of the 743 individuals observed 136 were normal. The daily counts show that the appearance of normals is due to the fact that the females were not virgins.

Virgin matings were made from these cultures, the results of which are contained in Table III. Of the 425 individuals of the F_1 from these cultures, 411 had noticeable W.S. markings and 14 appeared to be normal. In culture 63, from B, a male appearing to be normal was mated to a female showing W.S. only slightly. All the offspring were W.S.

The crosses N $\times$ W.S., shown in Table III, do not give the results expected. The total number of individuals obtained from all such matings during the experiment, many of which were from other crosses and not included in this table, was 471. One hundred and thirty-eight of these were W.S. This gives practically a 3 to 1 ratio. From the breeding experiments to date no explanation can be given for this unexpected ratio.

Table IV shows the results from culture 32, a N $\times$ N mating of beetles taken from stock 17. Note that two males in the F_1 were questionably normal, showing slight W.S. tendencies. They were mated (88) with normal sisters, and from the fifty-four offspring only one individual showed any indication of wide spacing. This indicates that individuals in the normal cultures may show slight variations in the spacing between the third and fourth spines, but when mated they breed true. This conclusion is not based on this one mating but upon several such matings of questionable individuals appearing in other cultures not included in Table IV. Beetles appearing to be normal or nearly so were found in the W.S. cultures. The mating of these individuals gave W.S. off-

TABLE III

SHOWS THE DESCENDANTS OF THE ORIGINAL W.S. PAIR.

	Normals			Variations		
	♂♂	♀♀	Totals	♂♂	♀♀	Totals
P_1.						
W.S. ♂ × W.S. ♀	32	35	67	36	19	55
(Not virgin)						
F_1 matings.						
Each culture was made up with 4 W.S. ♂ ♂ × 4 W.S. ♀ ♀. (Not virgin)						
A.	4	23	27	78	82	160
F_2 matings.						
59. W.S. ♂ × W.S. ♀	0	0	0	9	15	24
F_3 matings.						
110. 2 W.S. ♂ ♂ × W.S. ♀	0	0	0	22	26	48
112. 2 W.S. ♂ ♂ × 4 W.S. ♀ ♀	0	1	1	11	10	21
Cross.						
126. N ♂ × 3 W.S. ♀ ♀	17	12	29	2	5	7
Cross.						
129. 2 N ♂ ♂ × 2 W.S. ♀ ♀	0	1	1	2	0	2
60. W.S. ♂ × W.S. ♀	0	0	0	5	7	12
106. W.S. ♂ × 2 W.S. ♀ ♀	0	0	0	23	22	45
Cross.						
117. N ♂ × 2 W.S. ♀ ♀	2	6	8	1	2	3
Cross.						
135. W.S. ♂ × N ♀	8	12	20	4	1	5
84. W.S. ♂ × W.S. ♀	0	0	0	1	1	2
105. 5 W.S. ♂ ♂ × 5 W.S. ♀ ♀	2	1	3	97	103	200
111. 4 W.S. ♂ ♂ × 5 W.S. ♀ ♀	2	1	3	18	16	34
B.	21	21	42	76	73	149
42. W.S. ♂ × W.S. ♀	1	2	3	10	12	22
63. N (?) ♂ × W.S. ♀	0	0	0	3	7	10
Cross.						
120. 2 W.S. ♂ ♂ × 3 W.S. ♀ ♀ (♂ ♂ from 61)	0	1	1	9	12	21
139. W.S. ♂ × 2 W.S. ♀ ♀	0	0	0	31	38	69
90. 2 W.S. ♂ ♂ × 2 W.S. ♀ ♀	3	1	4	3	9	12
C.	15	14	29	90	104	194
41. W.S. ♂ × W.S. ♀	0	0	0	13	9	22
113. 3 W.S. ♂ ♂ × 4 W.S. ♀ ♀	0	0	0	11	14	25
61. W.S. ♂ × W.S. ♀	0	0	0	9	13	22
68. W.S. ♂ × W.S. ♀	0	1	1	17	17	34
Cross.						
92. W.S. ♂ × N ♀ (♀ from 34)	5	11	16	16	8	24
Cross.						
76. W.S. ♂ × W.S. ♀ (♀ from 61)	0	0	0	13	20	23
D.	8	30	38	38	67	107
40. W.S. ♂ × W.S. ♀	0	0	0	9	18	27

spring. These questionable appearing "normals" in the W.S. cultures are then merely variations in the spacing toward the normal.

TABLE IV

SHOWING THE RESULTS FROM CULTURE 32, A N×N MATING

	Normals			Variations		
	♂♂	♀♀	Totals	♂♂	♀♀	Totals
P_1.						
32. 2 N♂♂×N♀♀	44	57	101	(2)	(1)	(3)
(From stock 17)						
F_1 matings.						
Cross.						
137. 2 L♂×N♀	1	11	12	0	0	0
(♀ from 102)						
Cross.						
132. 2 N♂♂×2 N♀♀	9	8	17	0	0	0
(♂ from 54)						
54. N♂×N♀	14	21	35	0	0	0
F_2 matings.						
98. N♂×N♀	4	6	10	0	0	0
103. 2 N♂♂×2 N♀♀	3	7	10	0	0	0
55. N♂×N♀	14	21	35	0	0	0
102. 3 N♂♂×4 N♀♀	4	14	18	0	0	0
66. N♂×N♀	2	3	5	0	0	0
77. N♂×N♀	12	14	26	(2)	0	(2)
119. 4 N♂♂×4 N♀♀	4	6	10	0	0	0
136. N♂×N♀	4	3	7	0	0	0
79. 2 N♂♂×2 N♀♀	10	10	20	0	0	0
80. W.S. (?) L♂×N♀	7	8	15	0	(2)	(2)
83. 2 N♂♂×2 N♀♀	1	1	2	0	0	0
88. 2 W.S. (?) ♂♂×2 N♀♀	27	27	54	(1)	0	(1)
116. 2 N♂♂×2 N♀♀	5	7	12	(1)	0	(1)

While removing the parents from a culture (93) it was noticed that the supposedly normal beetles had long prominent first and sixth spines. This was the first time this had been noticed, but in looking over some of the other cultures individuals having prominent first and sixth spines were found mixed in with the normals. The parents of the culture 131, another supposedly normal culture, also had this peculiarity (see Fig. 4). The experimental breeding is incomplete, but these two cultures, shown in Table V, indicate that this is an heritable character. It is like the W.S. character, however, and is variable and sometimes difficult to determine.

TABLE V

SHOWING THE RESULTS OBTAINED FROM CULTURES WHOSE PARENTS HAD PROMINENT FIRST AND SIXTH SPINES (P)

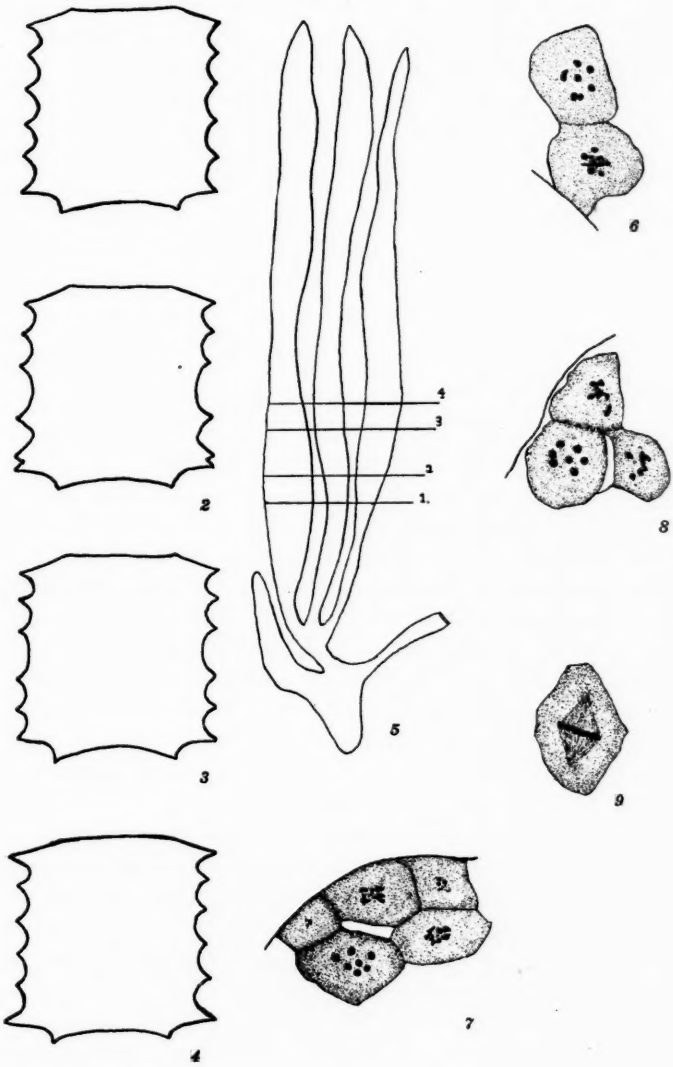
	Normals			Variations		
	♂♂	♀♀	Totals	♂♂	♀♀	Totals
P_1.						
93. P♂ × P♀	(1)	0	(0)	20	32	52
(From 38)						
F_1 mating.						
128. 3 P♂♂ × 4 P♀♀	0	0	0	4	12	16
131. P♂ × P♀	0	0	0	12	11	23
(♂ from 74, ♀ from 56)						

In order to make a cytological study of the beetles, to determine if possible the number of chromosomes, the breeding experiments were discontinued at this point.

CYTOLOGICAL

With the characters necessary for an insect suitable for experimental genetics, mentioned at the beginning of this paper, one might add that it is most desirable that the chromosomes be few in number and large enough to be studied. The difficulty in the cytological work has been that of finding a fixative suitable for the chromosomes in the insect. A modification of Bouin used by Carothers (16) proved to be excellent. The sections were cut 5 μ in thickness and stained with iron hematoxylin. The best definition was obtained with the short method, *i.e.*, by leaving the sections in iron alum for two to three minutes, washing fifteen minutes, then staining for four minutes. The destaining process takes from one to two minutes (Lee, 28).

Since it is difficult to remove the gonads in good condition, serial sections were made of the advanced larval stage, prepupal stage, pupae of several ages and young adults. The hard shell of the older adults makes them impossible to section. In the stages up to the mid-pupae the gonads were small and failed to show any stages of maturation with definite chromosomes. The young adults proved to be the best material, since at this age


4
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1.
2
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6
8
9
7

all stages from the spermatogonia to the mature germ cells can be found. The female has proved to be unsatisfactory for chromosome study.

The gonad itself is a long trilobed organ, extending nearly the full length of the abdomen in both sexes (see diagram, Fig. 5). At the posterior end of the testis, area 1 in the diagram, great masses of spermatozoa occur. Next comes the area (2) of spermatids. Anterior to this area (3) one finds secondary spermatocytes. The next region (4) contains the primary spermatocytes. The remainder of the testis is made up of spermatogonia and a few scattered groups of primary spermatocytes.

As the primary spermatocyte divides to form the secondary spermatocyte the chromosomes are large, due to the fusion of the homologues. This gives the haploid number. A section through the equatorial plate shows these double chromosomes clearly. There are seven globular chromosomes of practically equal size. Figs. 6, 7 and 8 show sections through the equatorial plate. Fig. 9 shows a section through a dividing primary spermatocyte perpendicular to the equatorial plate. Because of the minuteness of the chromosomes the diploid number in the somatic cells has not been determined, but there would be a maximum of 14 and a minimum of 13, depending on the mechanism of sex determination in this beetle.

SUMMARY

In summarizing the work done on *Oryzaephilus surinamensis* it may be said that it presents possibilities for further investigation. It is a suitable insect for experimental genetics for:

(1) Although the variations are somewhat indefinite two have been found to be inherited.

(2) It lends itself to laboratory breeding.

(3) The males and females can be distinguished easily.

(4) Under optimum conditions a generation is obtained every thirty to thirty-four days.

LITERATURE CITED

Back, E. A., and Cotton, R. T.
1926. "Biology of the Saw-toothed Grain Beetle, *Oryzaephilus surinamensis* Linné," *Jour. Agri. Research* 33: 435–452.

Carothers, E. E.
1917. "The Segregation and Recombination of Homologus Chromosomes as Found in Two Genera of Acrididae (Orthoptera)," *Jour. Morph.* 28: 445–522.

Lee, B.
1928. "The Microtomist's Vade-mecum." Ninth ed., 315–317. Philadelphia.

DO SOUTHWESTERN QUAIL REQUIRE WATER?

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IN *Science*[1] Grinnell has discussed the diminishment of California quail on certain areas of southern California with which he is familiar, checking off the various possible or probable responsible factors, and concluding that the water factor is the critical one. He stresses the probability that this factor is most vitally active "in a very short segment of the life cycle of our quail. Briefly, a brood of newly hatched quail must find itself within walking distance (walking distance, be it emphasized, for the *little* quail) of water to drink by them, within a few hours of hatching. Anticipating this need, the old quail seek nesting sites accordingly. For without water the young are doomed to perish, if the time of hatching happens to fall within a rainless or dewless period of weather."

While hesitating to question the theory of so eminent an ornithologist as Dr. Grinnell, I feel that certain more or less general observations in southern Arizona and my own conclusions based thereon should be set forth. The writer would not presume to speak for the particular areas of southern California known to Grinnell and not to himself, but in the article referred to the theory is extended to a generalization for the arid southwest. During more than ten years I have carried on work in this region which has taken me afield at all seasons of the year; and I have been much interested in the matter of water requirements of our so-called "desert" animals.

Much work has been done on the Santa Rita Range Reserve, a fifty square mile area of regulated grazing range thirty to forty miles south of Tucson, Arizona. I

[1] "A Critical Factor in the Existence of Southwestern Game Birds." Grinnell, Joseph, *Science*, Vol. lxvi, 1927, pp. 528–29.

am fairly familiar with all parts of this range and with the locations where water is available and have a detailed familiarity with much of it. Watering places for that portion of the reserve on which quail are chiefly found are but six in number, one of these at a ranch, and these represent not a decrease in available water, but an actual increase, since water is piped for long distances to most of them. On the other hand, this water is not available to little quail and scarcely so to adults, except if and when there is leakage or splashing to form muddy, cattle-trampled pools. Such pools are perhaps generally available—let us assume that they are always so. Even so, one can certainly locate many areas which are two miles or more from water and probably some areas are as much as three miles distant. Quail occur all over this range; and I am sure that on many areas elsewhere in southern Arizona they are found several miles from water. State Game Warden Doze, of Kansas, says[2]: "Our quail live in the sand hills of the southwest four or five miles from water for long periods of time. It is so dry in these sand hills that there is no dew in the grass yet the quail and prairie hen seem to exist and increase." But to confine ourselves to the range reserve, the quail population there is a large and flourishing one and seems to be fairly evenly distributed so far as availability of water is concerned. Suitable "cover" (from birds of prey), shade and food supply cause to some extent a localized grouping. Further, one may spend days on this area without seeing a covey of quail in flight, unless they are flushed, and flights are then short. Grinnell definitely implies flights of quail to water. Such flights do not occur with *Lophortyx gambeli* or *Callipepla squamata*. If they either flew or walked to water regularly a most noticeable massing of the birds would necessarily occur; but much massing does not occur. The same reasoning applies to jackrabbits, which are never found congregat-

[2] Doze, in Bulletin of Amer. G. P. A.; quoted in *New Mexico Conservationist*, Mar., 1928.

ing about water holes. Doves on the other hand are very dependent upon water supply and one notices not only their massing at water holes and seepages, but their flights to and from water.

To say with certainty from what food sources quail secure sufficient moisture to maintain life is perhaps not possible. Results of the Biological Survey investigations[3] on the food of our two species are meager. Fruit is a very small item in the food of Gambel quail as reported (twenty-eight stomachs), yet I am reasonably certain from cursory examination of crops in hunting season that at that time fruit is taken in larger percentage than reported. Leaves and plant shoots (succulent material) form 63.74 per cent. of the food, indicating the probable source of water. I have watched scaled quail eat heartily of stinging ants as the latter fared forth in droves at sunset, and we find (*loc. cit.*) (forty-seven stomachs) that they eat more insects and less succulent vegetable matter than the Gambel quail.

While the proportions of fruit, insects and succulent vegetable matter in the diet of the California quail (601 stomachs) differ from both Gambel and scaled quail, it seems doubtful that a significant difference as regards their need for water could be deduced therefrom. Therefore, no such analysis will be attempted.

Nothing is known of the food habits of very young quail. It may well be that a much larger proportion of insects is taken, or, it may be that the greater success of the young in favorable years is due to the greater abundance of succulent vegetation furnishing necessary water.

I have known of Gambel quail in the arid foresummer of a "bad year" concentrating on a field of small melon plants to such a degree that a shotgun guard was stationed to repel the invaders, and, under similar conditions, of destruction of young cotton plants. The obvious need was succulent vegetation. These occurrences

[3] Judd, Sylvester D., "The Bobwhite and other Quails of the United States in their Economic Relations." U. S. D. A. Bur. of Biol. Survey. Bull. No. 21.

were right in the normal breeding season, though I am not informed whether young were present. I have just had a male Mearns quail (*Cyrtonyx montezumae mearnsi*) which with a female reached me in November, 1927. At that time these quail were in juvenile plumage, but practically full grown. They were placed for observation in a small cage on my own back lot. Water was provided at first, but they appeared to be oblivious to it, and after a few days the pan was removed. From then, say December 1, until February 15, 1928, those quail had no water supply. The winter season had been one of low precipitation and no water whatever remained on the ground or in the cage after the infrequent rains. They throve and assumed adult plumage on a diet consisting mainly of seeds (wheat, sunflower, cracked grain, cactus seeds and a very few acorns), with occasional locusts in December, and, at intervals, not daily, boiled egg or bits of apple. On the latter date the female (during a snowstorm, and in my absence) perished. Shelter was available, and cause of death a mystery. Certainly lack of water was not the cause, for the best water supply of the period was then available. This species, it may be remarked, was not included with the other two because its habitat is at elevations where water is more frequently available. The male lived and thrived under the same conditions until March 31, when it was placed in the university aviary.

Now as to nesting, while observations on this are not so numerous as on the coveys of adults, there does not appear on this range reserve any reason to believe that nests are congregated about water supplies. Were that the case, then an abundance of adult birds should be noted in restricted areas during the nesting season and such is not the case. I once saw on August 11 a scaled quail's nest in one of our experimental enclosures on the reserve, a location at least two miles from water in any direction. Not even in the rainy season do pools remain for more than a few hours after a rain on the natural sur-

faces. (In borrow pits along roads water accumulates, but quail were there before roads.) It is wholly unlikely that newly hatched quail travel two miles or one mile to water—and again, one doesn't find them so congregated. I believe from observation that a given covey of quail keep, normally, to a certain somewhat limited range, feeding out in one direction in the morning, resting in thick shade during the middle of the day, and back in the afternoon. If the entire breeding population of quail on the fifty square miles of the Santa Rita Range Reserve were concentrated in the nesting season about the half-dozen stock watering places, I doubt that men or cattle could avoid stepping upon the nests; and I believe a number of biologists and ornithologists who have done field work there will bear me out in my deductions.

Further, dew is not the answer for this question. For a few nights following a rain dew occurs, but during most of the spring nesting season it is chiefly notable for its absence. A series of humidity records from a recording hygrothermograph bears this out.

Failure of many quails to nest in the normal spring breeding season following extremely dry winters has been remarked by myself and other observers. However, the stock watering places are then functioning—kept so by the efforts of the cattlemen. The problem is explicable in my opinion, on absence of succulent vegetation, which results, we believe, in marked decrease of breeding in jackrabbits (whether a vitamin lack or purely lack of water we do not know). Following a spring season of this type, if summer rains are normal and green vegetation springs up, July and August nesting of quail (and breeding of jackrabbits) occurs. Under such circumstances was the August 11 nest noted; and in such years the hunters find many quail too small for hunting on the opening date, October 15.

On April 6 I took the trouble, since the nesting season was near at hand, or already begun, to investigate three of these watering places on the Santa Rita Reserve. Water

was available on the ground for even young quail at all three tanks. At the first, the originally scanty cover has been trampled out by stock until there is scarcely a possible safe nesting site within four hundred yards of the water. Not one quail was seen or heard near by. About the second tank (established two years or less) there is still considerable brush cover within the four hundred yard radius. Further, this tank is located (on a pipe line) on a wash which I have known for several years as good quail hunting ground. Within the four hundred yards I found exactly two quail—probably a pair. Somewhat further distant were two more. The third tank visited has been in use for stock as long as I have known the reserve (ten years), is situated in the bed of a very large and deep wash offering fine winter shelter for stock and birds and the area has been in the past very badly trampled. Few stock are watering there now. Up and down this wash for a long distance has been good quail ground, but on the date mentioned I saw two quail at the water, and estimated from glimpses of birds and calls heard not to exceed a dozen within four hundred yards. On following down the wash three-quarters of a mile rather numerous quail were glimpsed or heard, and while eating lunch three-quarters of a mile or more from the water, quail were heard abundantly. That most of the quail seen on that date were in pairs indicated preparation for nesting, but there was no evidence of a competition for sites near the watering places. During the course of not less than twenty miles of driving in the reserve or immediately contiguous and similar territory quail were seen, as usual, well scattered over the country.

Lastly, let us see whether by analogy with domestic fowls we may shed some light on this problem. I am informed by our poultry authorities that it is common knowledge and regular practice among poultrymen to ship just-hatched baby chicks without either food or water for periods of seventy-four hours—three full days. The postal regulations allow ninety-six hours for such

shipments. Our department of poultry husbandry found last year that chicks would live eleven days without either food or water. Yet the ancestral jungle fowl comes from a less arid country than Arizona, and under domestication they are well provided with water! In view of these facts the field observations and deductions seem almost superfluous.

As a hunter myself, I shall have to say that in my opinion hunting (legal or illegal) is, or has been (perhaps years ago) the chief factor delimiting the quail population in the arid southwest.

THE CULTURE OF LARGE FREE-LIVING AMEBAE

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IT is only within relatively recent years that methods for the mass culture of the larger forms of free-living amebae have been published. This seems all the more remarkable in view of the fact that different species of large amebae of this kind have been known for nearly two centuries. Among the contributors to our knowledge of ameba-culture since 1900 may be mentioned the following: Stole (05), Parker (15), Schaeffer (16), Hyman (17), Taylor (18, 20, 24), Taylor and Hayes (21), Edwards (23), Levy (24) and Botsford (26). The writer has bred in mass culture for the past four and a half years one of the common large free-living amebae, *viz.*, Amoeba dubia Schaeffer,[1] and for the past two and a half years also Amoeba proteus Pallas (Leidy). As the method used differs fundamentally from the majority of those previously published and, in certain respects, from any other published account and as it has been thoroughly tested in practice it seems of value to give the present statement and discussion of the technique used.

In beginning a culture of ameba the first requisite is to establish in the laboratory an initial growth of the organisms obtained from some natural source. The sources of amebae in nature have been published so frequently that it seems unnecessary to go into detail on this point.[2] Of the two species the culture of which is described in this paper the writer has found both reasonably easy to obtain in ponds in the vicinity of Cambridge and at Woods Hole, both in Massachusetts. Amoeba proteus has been found in cultures from natural sources more frequently

[1] The nomenclature proposed by Schaeffer (16) is adopted here.

[2] For accounts of the habitats in which large amebae may be found the reader is referred to papers published by Schaeffer and Taylor.

than Amoeba dubia, although the latter species was found to be predominant in small streams and ponds in the Harvard Botanical Garden and vicinity at Soledad, Cuba.

The method used to establish a culture of amebae from material supposed to contain these organisms is essentially as follows: The collected water and included plant and animal material both living and dead are placed in finger-bowls, using in each bowl a volume not exceeding 30 to 40 cc. This is diluted gradually from day to day with a non-toxic distilled water by putting in about 10 cc each day until the total volume in the finger-bowl is about 70 cc. These cultures are allowed to stand and are examined every few days. If amebae are present it has been usual to find that they become abundant within a month and frequently within ten days to two weeks. If the quantity of organic material is not sufficient to sustain the other protozoan life which develops in such a culture small quantities of nutrient substances may be added. The chief organisms to be avoided in such cultures are small crustacea, either copepods or ostracods. The writer is in entire agreement with Taylor and Hayes (21) that amebae will not grow in the presence of these crustaceans. Oligochaetes frequently flourish in such cultures but not to the great detriment of the amebae, and when it is desired to subculture from these original cultures the worms are rather easy to leave behind.

As soon as amebae become well established in the diluted finger-bowl cultures the following procedure is recommended. About 5 cc of the medium containing amebae and other smaller organisms are taken from the finger-bowl and put in a Syracuse watch glass, using for the purpose a medium-sized pipette, the selection being made by use of a dissecting binocular microscope. Such a microscope is an indispensable accessory during the entire process of establishing ameba cultures. To the selected sample in the watch glass is added gradually, *i.e.*, in the course of a few days, 5 cc of distilled water

and at the time of transfer a small piece of sterilized timothy hay of a dry weight of approximately .02 g. (the length of such a piece taken from a clean medium-sized stalk of hay varies between 15 and 20 mm). In a period varying from one to two weeks amebae will either thrive or disappear in such cultures. The practice has been to begin as large a number of such watch glass cultures as convenient, since the development of individual cultures varies extremely. Amebae from thriving cultures may be now removed to finger-bowls. The method in this case involves the dislodgement of the amebae from the bottom of the watch glass, which may be done by forcing a stream of the culture medium against them with a pipette or by using a wash bottle. In this transfer all the medium and contained organisms are put in the finger-bowl. Add distilled water to this transferred medium to bring the volume of medium in the finger-bowl to approximately 30 cc. At the same time add hay, sterilized by boiling three to five minutes, having a dry weight of .06 g. To this also may be added a wheat or oat grain (dry weights, respectively, of approximately .03 and .02 g.) sterilized in the same manner. Such proportions of nutrient material and water have been found most appropriate in beginning an ameba culture. At intervals, varying from five to ten days, 10 cc of distilled water should be added, and hay, which has been freshly sterilized, as previously mentioned, should also be added according to the condition of the culture. As a rule it has never been found advisable to add at one time more than .06 g. of hay by dry weight to such cultures. The total volume to which this culture should be brought by this slow addition of water and sterilized hay must not exceed 65 to 70 cc. Once well established, such a culture should contain thriving amebae for a period of at least one month. This, of course, varies with individual cultures.

To subculture a culture of this type when it has reached a climax in numbers of amebae present various

methods may be employed. The period at which the greatest number of amebae is present is easily found by periodic examinations under the dissecting binocular microscope. If it is desired to continue the culture in the same dish somewhat less than half of the culture medium may be poured or siphoned off directly, since as a rule the amebae or the majority of them will be found on the bottom. The remainder may then be mixed up thoroughly, thus dislodging the amebae from the bottom, and approximately half of the amebae and the organisms serving as food may be removed with a pipette. To the remainder may be added, gradually as before, distilled water and hay in the quantities mentioned. A new subculture may be made from the excess amebae and food organisms from the finger-bowl used for the first subculture, the procedure being precisely as previously described. This method is in essence similar to the modification described by Botsford (26), which consists of shaking up the amebae and pouring half of the initial culture into a second finger-bowl with the addition of fresh spring water and nutrient material to each.

If large numbers of amebae are desired many subcultures may be made by picking out from fifty to one hundred amebae from a thriving finger-bowl culture and placing these together with the surrounding medium from which they came in another finger-bowl. To this, depending upon the volume now present in the finger-bowl, 10 to 30 cc distilled water and .06 g., dry weight, sterile hay may be added at once. These cultures are then worked up to a 65 to 70 cc volume as described.

The use of Syracuse watch-glass cultures has definite advantages for class work. Small subcultures may be made at any time, using this type of dish. About three to four cc of medium containing amebae and surrounding organisms are placed in the watch glass and an equal quantity of distilled water plus sterilized hay with a dry weight of about .02 g. are added. These cultures are made up a day or so before class use and are suitable for

study directly with the low power (16 mm objective) of the compound microscope. Since the majority of such cultures will continue to live and flourish for at least ten days and not infrequently for a month or more they furnish an opportunity for the study of ameba in a suitable environment. The life activities are thus studied on normal typical animals. This method is particularly valuable for a study of the process of locomotion and of ingestion of food. The writer has records of students who have witnessed the ingestion of thirteen Chilomonas within a period of fifteen minutes. Frequently the process of fission is observed by students in such cultures. At the end of a study period of a week there are thus many more amebae available for study than those originally supplied.

Some idea of the length of time in which an ameba culture may be kept in good condition in the same finger-bowl may be had from the following account taken at random from observations made during the early part of this work on culture method. Finger-bowl culture number 5 of A. dubia was begun on September 23, 1924, from a culture obtained from a pond in the vicinity of Cambridge. This culture was kept until December 14, 1924, when it was discarded. The immediate cause of discontinuance of number 5 was due to infection with Cyclops, which entered the culture through the experimental use of unsterilized pond water. Culture number 37 was begun from culture number 5 on November 2, 1924, and amebae were grown continuously in the same dish until June 9, 1926, when this culture was discontinued before the writer left Cambridge for Woods Hole. At this time amebae were still living and gave every promise of continuing to live had the culture been cared for according to the method just described. This period, slightly over two years and seven months, represents the longest period during which any culture has been bred continuously in the same dish by the writer, and the history of this culture shows clearly that there was no apparent

reason why it could not have been continued indefinitely with proper attention. Subcultures from this and similar cultures have been kept in a thriving condition until the present time (June, 1928) by using the method described.

CONDITIONS AFFECTING THE GROWTH OF AMEBAE IN MASS CULTURE

That amebae may be grown successfully in almost any kind of water is shown by methods previously published. Thus Taylor (21) used boiled rain water, although she stated that tap-water if it does not contain substances harmful to amebae may be used. Schaeffer (16) prepared his cultures with the pond water in which the amebae were found originally. Hyman (17, 25) does not state the source of the water used. Levy (24) used distilled water and Botsford (26) following in part the method advocated by the writer used spring water. Although it has been stated earlier that a non-toxic distilled water has been used in the present method the writer has made thorough trials, using a great variety of waters, including distilled water prepared in pyrex glass vessels in the laboratory, commercial distilled water (Pureoxia), pond water and tap water as supplied to the zoological laboratory in Cambridge. All these, with the exception of the distilled waters, have been used both boiled and unboiled. As a result of these trials no great advantage has been found in the use of any particular kind of water. It is, however, always desirable to continue in the cultures to cultivate only those organisms which are already living with the amebae. To insure this it is necessary to boil all pond, spring and tap waters before using them for culture purposes. One advantage of distilled water lies in the fact that it does not contain any nutrient materials, and this helps to keep the necessary low concentration of nutrient material in cultures in which it is used. In general, provided only that it is non-toxic, the kind of water used does not seem to be an important factor in the culturing of the common large amebae.

All the cultures have been grown at room temperature, which has varied from 14.5° to 24° C. No attempt has been made to ascertain the optimum temperature for the growth in mass culture of either of the two species concerned. Taylor (21) stated that the optimum temperature was found to range from 54° to 60° F. (12.2–15.5° C.). Although it has been found that amebae will grow and thrive at the higher range of the temperature given above, the writer agrees with Taylor that the lower range is more nearly the optimum for these species. The present work demonstrates, however, that ordinary room temperatures are entirely suitable for growth of amebae.

So far as light is concerned in this work care has been taken to exclude direct sunlight from the cultures. A northern exposure gives entirely suitable light conditions for mass culture growth. No reduction of light from that which normally entered the room has been made except in the case where it was desired to retard the growth of green algae.

The hydrogen-ion concentration of the different kinds of water used in the cultures varied in general between the values 6.4 and 7.2. A large number of determinations of the p^H of ameba cultures at various ages in their history have been made, using colorimetric methods. It has been found that in cultures of this type the hydrogen-ion concentration remains relatively constant. A culture which thrives well from the beginning has been found to have as a rule a p^H of from 6.8 to 7.1. This is a somewhat higher value than that of 6.6 reported by Taylor (24). In cultures in which green algae are growing the p^H is, as to be expected, somewhat higher and ranges from 7.2 to 7.4. A further significant fact is that in cultures of the type described here there is little difference in the p^H in cultures of equal age which have been subjected in general to the same treatment, but in which the amebae are in very different physiological condition. The initial somewhat lower value of the p^H in hay infusion cultures found by Bodine (21) and stated by him, in agreement

with the earlier work of Peters (07) and Fine (12), to be due in part to the initial heavy bacterial growth and in part to the acid-forming constituents of the hay is absent in the cultures described here. Since these cultures do not have a heavy bacterial growth at any time an increase in acidity due to this source is precluded. There is, however, a gradual slow rise in alkalinity as the cultures grow older, which is particularly marked when changes of culture medium are made only at long intervals.

Analyses of the dissolved oxygen content and of carbon dioxide in cultures both in a flourishing condition and when the amebae were dying have been made both for algal and non-algal cultures. These determinations were made in the morning with the room temperature at 20.8° C., the cultures at the time being exposed to diffuse light.[3]

CULTURES IN WHICH AMEBAE WERE DYING OR IN POOR CONDITION

Type of culture	Per cent. saturation oxygen	Parts per million CO_2	pH
Heavy algal growth	83	7	7.2–7.4
Scanty algal growth	73	7	7.3
Non-algal	72	9	7.1
FLOURISHING CULTURES			
Non-algal	71	6	6.9–7.0

It will be seen that only in heavy algal cultures is there a significant difference in the dissolved oxygen present. Since the cultures compared were all of the same age and had been subjected to similar treatment it is believed that there is no necessity for aeration of non-algal mass cultures of this type. Sufficient aeration occurs, due to the loose covering of the dishes, the relatively small amount

[3] Determinations of dissolved oxygen were made using a modified Winkler method with samples of 10 cc of medium. Carbon dioxide determinations were made directly by titration. The writer is indebted to Dr. E. Purkyne, graduate student in the Department of Sanitary Engineering, Harvard University, for aid in making these determinations.

of medium which is present at any time in the culture and the periodic changes in water content of the medium. A series of experiments was carried out in which a culture subdivided equally has had one half subjected to aeration for eight hours each day by slowly bubbling air through it, while the other half has been left untouched. Careful examination of these cultures each day for a period of two weeks showed no observable difference in the numbers or condition of the amebae thus examined. The result of these determinations as well as the experience of several years of culture of amebae has led the writer to conclude that, in cultures carried on in this manner, there is no need for extra aeration.

The staple food organism for both A. dubia and A. proteus has been the flagellate, Chilomonas paramecium, and this species has been present in nearly all the cultures grown. Associated with Chilomonas, although of less importance as a food organism, is the ciliate, Halteria grandinella. In addition to these protozoans cultures have been grown with many different combinations of organisms. In varying combinations the following organisms have been used throughout the course of the work:

Infusoria—Paramecium aurelia, Frontonia leucas, Spirostomum, Coleps, Euplotes patella, Euplotes charon, Stylonychia sp., Oxytricha sp. and Colpidium colpoda.

Mastigophora—Euglena sp., Monads, Entosiphon sp.

Sarcodina—Arcella vulgaris, Centropyxis aculeata, Amoeba dofleini (see Johnson, 28).

Chlorophyceae—Ankistrodesmus falcatus, Oedogonium sp., Dictyosphaerium sp., Scenedesmus sp. and Mougeotia sp.

Cyanophyceae—Calothrix sp.

Fungi—Dictyuchus sp.

Rotifera—Philodina roseola, Monostyla sp., Noteus quadricornis.

Nemathelminthes—Various free-living nematodes.

Annelida—Oligochaetes of several species.

Crustacea—Ostracoda (Cypris sp.) and Copepoda (Cyclops sp.)

Of this varied list of organisms the only ones found to be positively harmful to amebae are the crustacea and Dictyosphaerium. Oligochaetes, provided their multipli-

cation is not too great, live in the cultures without serious detriment to the amebae.

Concerning the value of green algae in ameba cultures the records of the writer show that their presence or absence makes little difference to the growth of ameba. Observation has shown that the algae enumerated do not serve in any important way as food for ameba. In old cultures amebae live on in small numbers for a longer time if algae are present and the algal growth is not excessive. On the other hand, the most successful growth so far as numbers are concerned has occurred in cultures free from algae. It should be noted, however, that only one of the green algae, Dictyosphaerium sp., has been found detrimental to the growth of ameba.

One species of fungus, Dictyuchus sp., one of the less known members of the Saprolegniaceae, has been commonly present in the cultures. This fungus grows readily on the grains of wheat or oats. Both spores and sporangia of this species are ingested by A. dubia and A. proteus. In cultures where Dictyuchus is growing luxuriantly amebae are usually found clustered on the hyphae.

The organisms listed have been present in varying combinations in the mass cultures, except those which were fed with Chilomonas only. Thus during the course of culture 37 the following organisms were present in the medium for varying periods—Chilomonas, Euglena, Paramecium, Ankistrodesmus, Mougeotia and Philodina. Of these, Chilomonas and Ankistrodesmus were present during the entire period.

The result of this long-continued mass culture of these two species of common large amebae has been to demonstrate beyond question that there are probably relatively few microscopic organisms with which these amebae will not live. The writer wishes to emphasize as strongly as possible that the most essential factor in the culturing of large free-living amebae is that the culture medium should not be so concentrated as to furnish too luxuriant

a bacterial flora. Amebae will not continue to live in the presence of heavy bacterial growth. If bacteria-feeding protozoa are present in such cultures their rapid multiplication provides conditions equally detrimental to amebae. On the other hand, there is a certain positive benefit in the presence of bacteria-feeding protozoa in an ameba culture. If the multiplication of such forms is seen to be going on too rapidly there is need for the dilution of the culture medium; if the medium will support such protozoa in sparse numbers amebae will in the great majority of cases flourish. Such protozoans as Paramecium, Frontonia, Spirostomum, Euplotes, etc., may thus be used as indicators of the fitness of the medium for the growth of amebae. Besides acting as an indicator there is also the probability that the pure bacteria feeder itself serves as an agent by which excess in the growth of bacteria is checked. Similarly, the rotifers of the species listed are equally valuable indicators of the fitness of the medium.

The writer wishes to emphasize the fact that his experience in the culture of these species corroborates fully their separation by Schaeffer (16). In all cultures and subcultures of A. dubia the characters marking this species are present in the offspring and in equal measure the same is true for cultures of A. proteus. In addition to the diagnostic features already adequately described by Schaeffer fundamental differences have been disclosed by microinjection studies (Dawson and Belkin, 28). Not only is the initial injection of small masses of oils more difficult, but extrusion of injected oils is much more common in A. proteus than in A. dubia. This, it is believed, is correlated not only with differences in the protoplasm of these two species but also with the greater thickness of A. dubia, which, when the organism is crawling freely, is, on the average, approximately 70 μ, as compared with 40 μ similarly measured in A. proteus.

Each species of ameba was collected from one source only and at one time. During the entire course of the

cultures no "depression" periods similar to those mentioned by Taylor (24) have occurred nor has any formation of cysts been observed during the periodic examinations of the cultures. This leads to the conclusion that, provided suitable environmental conditions are maintained, both Amoeba dubia and Amoeba proteus are capable of maintaining themselves indefinitely by binary fission. A view similar to this has already been expressed by Schaeffer (28).

This method of culture has some similarities in general with that given by Taylor (21, 24). Although wheat, when used, is in nearly the same proportion by weight as that given by Taylor, it has been found that entirely satisfactory results may be obtained by the use of carefully selected timothy hay in the quantities and proportions mentioned. Due to the slower disintegration of the hay such cultures are slower to develop and reach a climax of numbers of amebae than those containing wheat or oat grains; the growth, however, is surer and usually better sustained. Although use of this method of subculturing or of continuing an established culture has been found to insure the continuance of growth of amebae in a remarkably high percentage of cases, it is to be emphasized that considerable discrimination in the treatment of individual cultures is necessary. This, of course, is only obtained through actual experience. It has been successfully used, however, by a number of the writer's students who were previously without much experience in the culture of protozoa.

The description given here is thus an attempt to show as precisely as possible the conditions under which cultures of the common large free-living amebae, Amoeba dubia and Amoeba proteus, may be kept growing indefinitely, and, if so wished, in the same culture dish. One essential feature is that the amebae are supplied with an environment as similar as possible to that which they encounter in nature. The weak concentration of the culture medium so far as nutrient substances are concerned,

gradual changes in the medium when changes are necessary and the lack of a "prepared" medium are also fundamental features. The writer believes that his experience shows that amebae can be most successfully cultivated by allowing for the relatively slow simultaneous growth of the amebae and the necessary food organisms as well as others in the culture. In this respect the method is in contrast with that used by a number of investigators in which the nutrient medium is prepared and allowed to stand exposed to the air or inoculated to promote bacterial growth before amebae and other organisms are added.[4] In general, with appropriate modifications this method may be used for any protozoan and has been so used by the writer for several years.

LITERATURE CITED

Bodine, J. H.
1921. "Hydrogen-ion Concentration of Protozoan Cultures," *Biol. Bull.*, Vol. 41, p. 73.

Botsford, E. Frances.
1926. "Studies on the Contractile Vacuole of Amoeba," *Jour. Exp. Zool.*, Vol. 45, p. 95.

Dawson, J. A., and Morris Belkin.
1928. "The Digestion of Oils by Amoeba dubia," Proc. Soc. Exp. Biol. and Med., Vol. 25, p. 790.

Edwards, J. Graham.
1923. "The Effect of Chemicals on Locomotion in Ameba. I. Reactions to Localized Stimulation," *Jour. Exp. Zool.*, Vol. 38, p. 1.

Fine, Morris S.
1912. "Chemical Properties of Hay Infusions with Special Reference to the Titratable Acidity and its Relation to the Protozoan Sequence," *Jour. Exp. Zool.*, Vol. 12, p. 265.

Hyman, L. H.
1917. "Metabolic Gradients in Amoeba and their Relation to the Mechanism of Amoeboid Movement," *Jour. Exp. Zool.*, Vol. 24, p. 55.
1925. "Methods of Securing and Cultivating Protozoa. I. General Statements and Methods," Trans. Mic. Soc. Amer., Vol. 44, p. 216.

Johnson, Percy L.
1928. "Amoeba dofleini (Neresheimer) vs. Mayorella bigemma (Schaeffer)," *Science*, n. s., Vol. 68, No. 1752.

[4] *Cf.* Parker (15), Hyman (17), Edwards (23), and Levy (24).

Levy, Joseph.
1924. "Studies on Reproduction in Amoeba proteus," *Genetics,* Vol. 9, p. 124.

Parker, J. B.
1915. "A Method of Obtaining a Supply of Protozoa," *Sci.,* n. s., Vol. 42, p. 727.

Peters, A. W.
1907. "Chemical Studies on the Cell and its Medium. Part I. Methods for the Study of Liquid Culture Media," *Amer. Jour. Physiol.,* Vol. 17, p. 443. "Part II. Some Chemico-biological Relations in Liquid Culture Media." Same, Vol. 18, p. 321.

Schaeffer, A. A.
1916. "Notes on the Specific and Other Characters of Amoeba proteus Pallas (Leidy), A. discoides spec. nov., and A. dubia spec. nov.," Arch. f. Protistenk. Bd. 37, p. 204.
1916. "On the Feeding Habits of Ameba," *Jour. Exp. Zool.,* Vol. 20, p. 529.
1928. "Recent Discoveries in the Biology of Ameba," *Quart. Rev. Biol.,* Vol. 1, p. 95.

Stole, A.
1905. "Über die Teilung des Protoplasmas im mehrkernigen Zustande. Nach den Untersuchungen an mehrkernigen Former der Amoeba proteus," Arch. f. Entwicklungsmech. Organ. Bd. 19, p. 631.

Taylor, Monica.
1918. "Notes on the Collection and Culture of Amoeba proteus for Class Purposes," Proc. Roy. Soc. Edinburgh, Vol. 20, p. 179.
1920. "Aquarium Cultures for Biological Teaching," *Nature,* Vol. 105, p. 232.
1924. "Amoeba proteus: Some New Observations on its Nucleus, Life History and Culture," *Quart. Jour. Micros. Sci.,* Vol. 69, p. 119.

Taylor, Monica, and C. Hayes.
1921. "The Technique of Culturing Amoeba proteus," *Jour. Roy. Micros. Soc.,* p. 241.

THE DISTRIBUTION OF *RUVETTUS*, THE OILFISH, THROUGHOUT THE SOUTH SEAS, AS SHOWN BY THE DISTRIBUTION OF THE PECULIAR WOODEN HOOK USED IN ITS CAPTURE

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WHILE working on the index volume of the "Bibliography of Fishes" some years ago, I became interested in this deep-sea fish, whose oil is a purgative. Presently I collected all the available data about this oil and published these in 1925.[1] While engaged in this study, I made many notes on the peculiar wooden hook used throughout the South Seas in its capture and projected a study of the hook. Specimens of these hooks were exhibited and reported on at the joint meeting at Washington in December, 1924, of the American Association for the Advancement of Science and the American Society of Zoologists, and a preliminary abstract of the projected research was published.[2] Later this work on the hook was completed and published.[3] From this monograph the data on the distribution of the hook are taken and here published. To this has been added certain informa-

[1] Gudger, E. W., "A New Purgative, the Oil of the 'Castor Oil Fish,' *Ruvettus*." *Boston Medical and Surgical Journal*, 1925, Vol. 192, pp. 107–111, text-fig.

[2] Gudger, E. W., "The Distribution of the Oilfish, *Ruvettus pretiosus*, in the Pacific Ocean, as Shown by the Distribution of the Peculiar Hook Used in its Capture." *Anatomical Record*, 1924, Vol. 29, pp. 128–129.

[3] Gudger, E. W., "Wooden Hooks Used for Catching Sharks and *Ruvettus* in the South Seas, a Study of their Variation and Distribution." Anthropological Papers, American Museum of Natural History, 1927, Vol. 28, pp. 199–348, 92 text-figs.

tion about either the fish or the fishing which has lately come to hand—chiefly in an article by Charles Nordhoff, of Papeete, Tahiti, who has collected extensive data on this subject.[4] All these data are here set forth to extend our scanty knowledge of the occurrence of this remarkable fish in the Central Pacific.

Ruvettus was first described from the Straits of Messina by Cocco in 1829, and later figured and more fully described by Cantraine in 1837 from another specimen from the same locality. Since this time it has been often taken along the northern shores of the Mediterranean from the Dalmatian coast to the Pillars of Hercules, in the Bay of Biscay and further south at Madeira and the Canaries. In the western Atlantic it is known from Cuba, Bermuda and off the Grand Banks of Newfoundland.

In the northern Pacific, it has been taken at Honolulu and off Tokio, and in the East Indies has been captured once in the Banda Sea. But for the central and south Pacific only one specimen has been caught and studied by an ichthyologist. This came about in the following interesting way.

In 1896 the Royal Society of London sent to Funafuti Atoll, Ellice Islands, a commission to bore into the reef to test Darwin's subsidence theory of atoll formation. The commission went *via* Sydney, Australia, and there the Australian Museum was asked to send along a representative to take part in the boring and to study the natural history of the island. The late Charles Hedley was chosen. At Funafuti, he heard from the natives of this peculiar fish and finally succeeded in getting one specimen. This he took back to Sydney, where it was identified by E. R. Waite[5] as *Ruvettus pretiosus.*

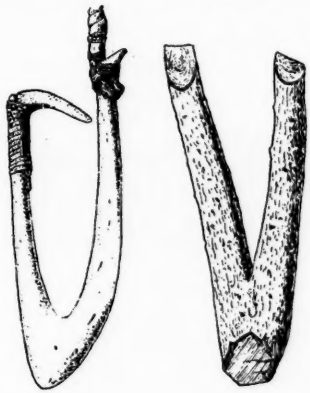
Here then is the only authentic specimen of *Ruvettus* known from the South Seas. Further knowledge of the

[4] Nordhoff, Charles, "Fishing for the Oilfish . . . *Ruvettus pretiosus,* at Atiu, Hervey Group, and Elsewhere in the South Seas." *Natural History,* 1928, Vol. 28, pp. 40–45. 6 figs.

[5] Waite, E. R., "The Fishes of Funafuti" [Supplement]. Memoirs Australian Museum, 1899, Vol. 3, pp. 539–544.

presence and distribution of the fish must be determined by the presence and testimony of its peculiar hook. This study had perhaps best be taken up by island groups, and for convenience these will be considered in the three great subdivisions of the islands of the central Pacific. Furthermore, so far as possible, we will work from east to west.

First, however, it will be well to give a figure of a typical *Ruvettus* hook. The one herein figured is the one brought back from Funafuti by Hedley. It is made from the fork of a bush or tree, the trunk furnishing the shank



1 1a

FIG. 1. A 9.25-inch wooden *Ruvettus* hook from Funafuti, Ellice Islands. After Hedley, 1897.

FIG. 1a. A fork of *vala vala* wood from Nukulaelae, Ellice Islands, from which a *Ruvettus* hook would have been made. After Hedley, 1897.

leg, the branch the barb leg. This fork is represented by the second figure, and study of the two figures will make clear the method of manufacture. The barb is separately made from a nearly right-angled fork. It and the top of the barb leg are spliced to fit and the barb is lashed onto the top of the barb leg. It is fitted to point obliquely inward and downward but slightly to one side of the shank.

The general plan of the hook is uniform through the whole of the South Seas, but the details vary with every group, and particularly in the form, splicing and lashing of the barb. Again these details are very definite for each group or region. So much is this so that hooks have come to me labeled from Group A, but after study of their details have definitely and assuredly been assigned to Group B. It does not seem necessary to enter into these details here.[6]

The fish is shown herein in Figure 2. It is a member of the family Gempylidae, living or at least caught at depths of from 80 to 400 fathoms—however, most commonly reported from the latter depths. In the South Seas it is caught only on moonless and windless nights, on the peculiar hook described above, and with a flying

FIG. 2. *Ruvettus pretiosus*, the oilfish—a mounted skin in the American Museum of Natural History. From a four-foot specimen, weighing 24½ pounds, taken at Bermuda, December 19, 1924.

fish or some other like succulent fish for bait. This bait is lashed fast to the top of the barb leg leaving the point of the barb free. *Ruvettus* has a large mouth and with this it takes in both bait and barb leg. The curious barb then catches the fish in the angle of the jaw or among the gill arches and holds it more securely than an American or European steel hook would.

Ruvettus IN POLYNESIA

The easternmost islands in Polynesia are known as the Paumotus or Taumotus. From this group (the Low

[6] For these details and for data and references to authors herein quoted in brief, the interested reader is referred to the larger paper listed in footnote No. 3.

Archipelago) two *Ruvettus* hooks have been recorded—one from Kakahina now in the Bishop Museum, Honolulu; the other a combination *Ruvettus*-shark hook from Fagatau, which the French naturalist Seurat distinctly says is used for taking *Ruvettus*. Furthermore, Louis Becke, who has written most about catching the oilfish, says that it was taken at Pukapuka (Danger Island) in his day.

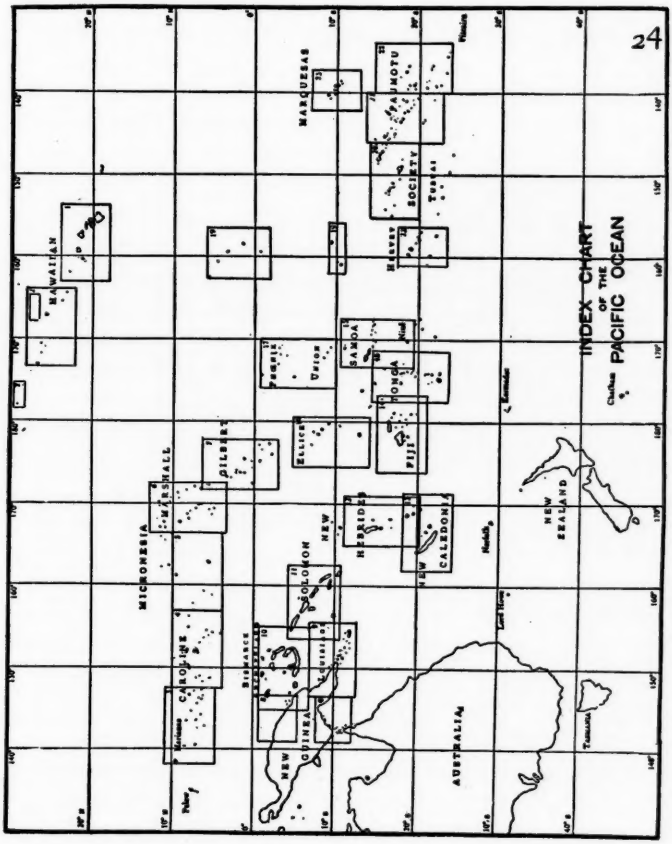


Fig. 3. A map of the Pacific Islands, on which may be located the islands or groups of islands from which *Ruvettus* hooks have been obtained. After Brigham, 1900.

The Society Islands lie west of the Paumotus and from them in general (*i.e.*, without designation of island) two hooks are recorded, while from Tahiti, in particular, six hooks have been figured and described. These vary from 2.75 inches to 15.25 inches long, and in weight from 2 or 3 ounces to 2 pounds 2.25 ounces. These latter huge hooks are combination *Ruvettus*-shark hooks (the others are more typical *Ruvettus* hooks), but they are definite proof of *Ruvettus* fishing here. This conclusion has been verified by Mr. Nordhoff, who writes that using native tackle he has with his own hands caught *Ruvettus* off the Tahiti reefs.

South of the Society Islands is the Austral Group, of which the island of Tubuai is possibly the best known. Two *Ruvettus* hooks in the Bishop Museum definitely testify to the presence of the fish here. Further, Mr. Nordhoff writes that he has positive information that the hook is to-day used to catch the oilfish at Rimatara and Rurutu in this group.

West of the Society and Austral Islands, lie the Cook or Hervey Group. From them but one *Ruvettus* hook is known—a specimen in the collections of the American Museum. It is a typical hook and may be taken as definitely establishing the presence of the fish in these islands. Confirmation of this conclusion will be found in the article by Mr. Nordhoff, elsewhere referred to, on the *Ruvettus* hook and fishing at Atiu and Mangaia.

North of the Hervey Group lie certain isolated islands from which no hooks have been reported, but at which it is alleged that *Ruvettus* has been taken. Thus Becke reports it from Manahiki or Humphrey Island, and in this he is confirmed by Nordhoff. The latter authority also says that the *Ruvettus* fishing is likewise carried on at the neighboring atoll of Rakahanga (Rierson Island), between which and Manahiki there is constant intercourse. From the neighboring island of Tongareva (Penrhyn), I described a number of shark hooks closely approaching

certain abnormal *Ruvettus* forms. Since then Mr. Nordhoff has sent me a sketch of the hook used here for taking the oilfish. And last of all these isolated islands is Washington Island to the far north (about 160° W. Long. and 5° N. Lat.) where Burnett took our fish (kind of hook not noted) in 1910.

West of the Hervey Group is the isolated upheaved coral island known as Niüe or Savage Island. Witnesses of *Ruvettus* fishing at this island are eleven hooks, remarkably similar in construction, so much so as readily to be picked out of a group of hooks. Some of these are arranged in "gangs" like trawl hooks of our Newfoundland cod fisheries. Furthermore, Becke says that many years ago he took the fish here.

The Samoan or Navigator Islands lie north of Niüe. From them there are two hooks believed to have been used to take *Ruvettus*. Furthermore, Krämer, whose knowledge of Samoan fish and fishing was very extensive, believed that the fish was caught at Manu'a. The evidence taken as a whole supports the belief that the oilfish is taken among the Samoan Islands.

The Tonga Islands lie west of and not far from Niüe. From this group there are five *Ruvettus* hooks in the collections of the American Museum, while from the United States National Museum there came to me a hook alleged to be from another island, but which on close study was shown to be from Tonga. Furthermore, Becke says that the fish was in his day taken there.

Ruvettus fishing has, by the hooks used, been nowhere better established than in the Tokelau or Union Group, lying north of Niüe and the Tongas. From the group in general, but mainly from Fakaofu (Bowditch Island) come twelve hooks with such marked peculiarities that they may be recognized at a glance as Bowditch Island hooks. The numbers of these hooks may be taken to indicate the abundance of the fish.

From New Zealand, far to the south, one *Ruvettus* hook has been (doubtfully) recorded. There seems little

reason, however, to doubt that the fish could be taken in these waters. Furthermore, the people are Polynesian and in all probability carried the peculiar hook south with them. Their shark hooks markedly approach the combination *Ruvettus*-shark type, which seems to strengthen the case.[7]

Last in Polynesia, we go far north to the Ellice Islands, where these hooks were first reported (Hedley, 1897). In the large paper referred to I described nine hooks from various atolls in this group. Lately Mr. Donald G. Kennedy, of Vaitupu in this group, has sent me four hooks, a description of fishing with these hooks (in which he has participated), and photographs of all the fishing gear used, including the hooks. (All these Ellice Islands hooks have very marked "family" characteristics.) *Ruvettus* fishing is perhaps more carried on in this group than any other. Becke so found it forty years ago.

To conclude the evidence for the occurrence of *Ruvettus* throughout the Polynesian Islands, it may be stated that in the Bishop Museum there are, among other objects in the J. L. Young collection, eight undoubted *Ruvettus* hooks obtained in various undesignated islands in Polynesia. It is very unfortunate that the origin of these can not be traced.

Ruvettus IN MICRONESIA

North of the Ellice Group are the Gilberts, and here fishing for the oilfish is likewise extensively practiced. Some twelve or thirteen hooks are recorded from this group, some typical, others transitional forms between typical *Ruvettus* and typical shark hooks. There is much intercourse between the Gilberts and the Ellice Group, and undoubtedly much interchange of fishing gear. Becke writes that in the early nineties he caught many

[7] Since the above was written, Mr. L. T. Griffin, assistant curator of the Auckland Museum, has published (Transactions of the New Zealand Institute, 1927, Vol. 58, pp. 146–148, pl. 15) a figure and description of a *Ruvettus* taken at White Island, Bay of Plenty. Five others were reported to have been captured. He makes a new species of this, *R. whakari*.

oilfish here at the island of Peru. Augustin Krämer also got the fish in this group and sent a head of it to the Stuttgart Museum, but no report was ever made on it.

Going northwest to the Marshall Group, we find one hook recorded (from the Bishop Museum collection), but it is enough to establish the fishing. Doubtless other specimens might be found in other museums, especially in Germany. These islands up to the time of the World War were under the domination of that country and the ethnology of the group has been carefully studied by German scientists.

Three hundred miles west of the Gilberts lies the solitary Nauru, Nawodo, or Pleasant Island. From it two *Ruvettus* hooks are known, and their describers, Hambruch and Thilenius, distinctly say that they were used for taking the "Purgierfisch." This fish is so well known to the natives that they have a cat's cradle figure which they call *eru*—purgative fish.

From the Mortlock Group of the Caroline Islands (Northern Mortlocks), the Australian Museum has a wonderful collection of *Ruvettus* hooks—ten in number, ranging in size from children's hooks, 3.25 inches long, to giants of 17.75 inches (weighing thirty-one ounces). These testify both to the great abundance and the enormous size of the oilfish caught in these islands.

Ruvettus in Melanesia

South of the Micronesian Mortlocks are the Melanesian Islands of the same name but sometimes also called Marcken or Marqueen Islands. In the Field Museum in Chicago and in the Australian institution are a total of six fine purgative fish hooks which plainly indicate the abundance of the fish in this group.

From the coral outliers fringing the Solomons on the east come hooks once used in taking *Ruvettus*—typical hooks; one from Nissan (Sir Charles Hardy Group) in the north; no hooks from Nuguria (Faed Islands) but

Krämer's word that he knew of the hook and its use there; and for Buka we have the authority of Krause (describer of the Nissan hook) that the same kind of hook is used at this island.

From Tasman and Ontong Java (Lord Howe Islands) comes a wealth of hooks—eleven in the Field Museum alone (most of which I studied)—and in addition figures and descriptions from Parkinson, Thilenius and Woodford, all of whom testify that the hooks were used only for taking the purgative fish—a favorite sport in these islands. All these hooks are huge ones, and Woodford states that these western Ruvettuses are from six to nine feet in length.

The southernmost of these outlying atolls is Sikiana or Stewart Island. The only hook from this—a very typical one—is in the Field Museum, but Woodford (formerly a British official in the Solomons) narrates that huge forms of the fish are taken at Sikiana.

In addition to the Melanesian hooks enumerated, several hooks were recorded from undesignated islands. These were not only undoubted *Ruvettus* hooks, but they bore all the earmarks of the strongly characterized Melanesian brand of oilfish hooks.

SUMMARY

There has been traced herein the distribution of the *Ruvettus* hook, and the writer believes the distribution of the oilfish also, from Fagatau in the Paumotu or Low Archipelago in the east (Long. 140° 52′ W.) to Nissan (of the Sir Charles Hardy Group) in the west (Long. 154° 10′ E.). This gives an east-west distribution of 64° 58′, or in round numbers 65°. Now Fagatau lies in about Lat. 16° S. and Nissan in about 4° 30′ S. The average is about 10° S. and on this parallel a degree has a value of about 68.13 miles. Hence the east-west range of the *Ruvettus* hook and fish is the tremendous distance of 4,430 miles.

The recorded north-south distribution reaches from the Mortlock Group in the Carolines to New Zealand, or from 5° 30′ N. Lat. to 40° S. (the line dividing New Zealand in halves is taken arbitrarily, since no point in New Zealand is specified for the solitary New Zealand hook). The north-south distribution then is 45° 30′ of latitude and, taking the value of the mean parallel of latitude as 68.8 miles, the distance amounts to 3,130 miles. Furthermore, there is known from Hawaii a huge combination *Ruvettus*-shark hook, and *Ruvettus* is to-day taken there. This, then, if counted, would add 10° 30′ more to the north-south distribution. However, the computation herein made will be restricted to the South Seas proper.

In this vast boundary of the south-central Pacific, a huge parallelogram 3,130 by 4,430 miles, the peculiar *palu* or *Ruvettus* hook is found in the majority of the island groups and in many isolated islands. In my judgment careful search would reveal hook or fish or both in all these islands. And of the hook itself, after prolonged study I endorse the saying of Hedley that "As characteristic an ethnological feature of its especial region as the boomerang of Australia or the bola of South America is the wooden deep-sea fish hook from the Central Pacific [used for taking the oilfish, *Ruvettus*]."

SHORTER ARTICLES AND DISCUSSION

THE CLASSIFICATION OF THE GENUS MONILIA

THE classification of the monilias has been the subject of much confusion. Castellani (1) has divided the genus into species by means of their biochemic reactions on carbohydrates; but, as he states, some of these reactions are not constant, and several species may, after a time, lose their power to ferment some of the carbohydrates. In a recent report (2) Gomes and Correa state that Castellani's classification based on carbohydrate fermentation seems deficient unless merely used for molds with well-established characters.

Boggs and Pincoffs, (3) in reporting a fungus allied to the genus Monilia, grew the fungus in gelatin stab culture, hardened the gelatin with formalin and made sections. They made no comparative studies. Ashford, (4) in reporting a monilia as the cause of Sprue, mentioned and laid great stress on the character of the growth of his monilia in gelatin stab culture, but he made no study of the microscopical structure of the growth.

The writer believes that these growths are constant and characteristic, and that they may be used as a basis for a morphological classification of the genus Monilia. A preliminary report of six members of the genus is herewith submitted. These differ in the size of the mycelial segments, in the shape of the moniliform clusters and in the size, shape and arrangement of the cells making up the clusters.

The fungus is grown in gelatin stab cuture using 10 to 15 per cent. gelatin for convenience of cutting, but for photomicrographic work a 5 per cent. gel will give a clearer medium. When the growth develops, 10 per cent. formalin in water is poured on the top of the culture to a depth of about one centimeter and allowed to act for three to five days. The culture tube is then broken off and the gelatin cut into thin sections free hand, mounted in water and examined without a cover glass. Microtome sections may be mounted, or stained and mounted, following the technique of Boggs and Pincoffs.

The sources of the six monilias studied were: albicans and psilosis—American Type Culture Collection; albicans W. & T.—Dr. F. W. Tanner (Dr. Tanner believed this to be closely allied, if not identical, with albicans Robin); richmondi and zeyla-

noides from the writer's collection and krusei—Dr. Aldo Castellani.

A brief description of the sections follows:

M. psilosis. No clusters were seen in any of the sections examined made from several different growths. The mycelium was very narrow.

M. albicans. Many clusters present. Cells round. Clusters isolated.

M. zeylanoides. Many clusters present. Cells round. Clusters arranged around the mycelium.

M. krusei. Many clusters present. Cells elliptical. Clusters do not show branching.

M. richmondi. Many clusters present. Cells elliptical. Clusters show branching. Cluster cells very small (1 x 4 microns).

M. albicans (W. & T.). Many clusters present. Cells elliptical. Clusters show branching. Cluster cells large.

The above characters may be arranged in the form of a key.

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LITERATURE CITED

(1) Castellani, Aldo.
New Orleans Med. & Surg. Jour., July, 1926.
(2) Gomes, J. M., and Correa, C.
Jour. A. M. A., p. 630, Feb. 25, 1928.
(3) Boggs, T. R., and Pincoffs, M. C.
Johns Hopkins Hosp. Bull., Oct., 1915, p. 354.
(4) Ashford, P. M.
Amer. Jour. Med. Sciences, Vol. 154, 1917, p. 166.
(5) Wallace and Tanner.
Amer. Rev. of Tuberculosis, Mar., 1927.

LINKAGE OF IVORY EYE COLOR WITH MINOR FACTORS FOR DEFECTIVE VENATION IN HABROBRACON

IN *Habrobracon juglandis* (Ashmead) normal black eye color, O, orange, o, and ivory, o^1, are allelomorphic (Chromosome I). Defects in the fourth branch of the radius vein occur frequently in the species. A certain factor, d II 95 (Chromosome II), causing defective veins in over 90 per cent. of the individuals of pure stock under standard conditions has been shown[1] to segregate independently of orange. Males of segregating generations bred in 1921 and 1922 from orange defective by type were type 1,208, defective 928, orange 1,212, orange defective 880. There are 42.763 ± 0.513 per cent. defective, significantly below the ex-

[1] Whiting, P. W., 1924, p. 31.

pected 50 per cent. due to somatic overlaps with normal. There are 50.615 ± 0.518 recombinations indicating no linkage.

F_2 males bred in 1924 from ivory defective by type were type 620, defective 406, ivory 369, ivory defective 641. Linkage is clearly indicated here, recombination types being only 38.065 ± 0.726 per cent. Since orange had previously segregated freely from d II 95 it was thought that possibly the two chromosomes had become fused. Percentage of defectives 51.424 ± 0.747, however, differing by 8.661 ± 0.907 from the corresponding percentage in the segregating generations from orange defective by type indicates that the apparent linkage is not due to chromosomal cohesion but to one or more minor factors for defective in Chromosome I.

Among the 1,026 black there are 39.571 ± 1.030 per cent. defective. This is somewhat lower (diff. $= 3.192 \pm 1.151$) than expectation when d II 95 alone is involved. If this difference is significant it may indicate that temperature during development was slightly lower than in the previous case. At any rate there are probably few or no crossovers between ivory and factors for defective in Chromosome I. On the basis of this proportion of defectives among the black, 400 of the 1,010 ivory should be defective on account of d II 95. Of the 641 defective ivory, approximtely 241 are therefore defective on account of Chromosome I factors and the 369 normal ivory are at least for the most part somatic overlaps.

The ivory defective stock used in the above crosses had been discarded, but counts of F_2 males from crosses of another line of ivory defective by type were made in 1925. There were type 353, defective 302, ivory 358, ivory defective 321. Recombinations are here 49.475 ± 0.923 per cent., indicating no linkage. F_2 males from orange defective by type counted in 1925 were type 192, defective 122, orange 208, orange defective 148, giving 49.253 ± 4.215 per cent. recombinations.

The ivory defective stock bred in 1924 evidently had minor factors for defect occurring in Chromosome I and lacking in our other defective stocks.

P. W. WHITING,
ANNA R. WHITING

LITERATURE CITED

Whiting, P. W.,
1924. "Defective and Freak Venation in the Parasitic Wasp, *Habrobracon juglandis* (Ashm.)," University of Iowa Studies in Child Welfare, Vol. iii, No. 1.